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JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

THE LEPIDOPTERISTS' SOCIETY

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The Lepidopterists' Society is a non-profit, scientific organization. The known office of publication is 1041 New Hampshire St., Lawrence, Kansas 66044. Second class postage paid at Lawrence, Kansas, U.S.A. 66044.

Cover illustration: Mature larva of *Ornithoptera goliath* Oberthür eating through the thick, corky stem of *Aristolochia crassinervia*, consuming the higher concentrations of secondary plant compounds that the stem of this vine contains. Original drawing by Mr. Michael J. Parsons, F.R.E.S., Hurst Lodge, Hurst Lane, Egham, Surrey TW20 8QJ, England.

CHECKLIST OF MONTANA BUTTERFLIES (RHOPALOCERA)

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ABSTRACT. A list of 177 species of butterflies (Rhopalocera) known to occur in Montana and the county where each specimen has been collected is compiled from records gleaned from university collections, resident collectors, published literature, non-resident collectors, some major natural history museums, and the author's collection.

This checklist has two basic purposes. The first is to present the latest information available on the species of butterflies occurring in Montana and to give their distributions. The second is to serve as a basis for soliciting additional records from non-resident collectors for inclusion in a larger work on Montana's butterflies, which is currently in preparation. This work will include photographs of all species, detailed distribution maps, collection records, life histories and food-plant information. Anyone who can add additional county records for any species is urged to contact me.

Seventy-three years have passed since the first and only attempt at a comprehensive treatment on Montana butterflies was published by M. J. Elrod in 1906, "The Butterflies of Montana," a 174-page illustrated bulletin. An abridged version of this is Elrod and Masters (1970). Early but restricted treatments are those of W. H. Edwards (1872, 1878, 1882b, 1883), Scudder (1875), and Wiley (1894). Papers treating only a species or group of species are Coolidge (1906, 1909), Clench (1944), Daly (1964), W. H. Edwards (1882a, 1886, 1890, 1894), Field (1936a, 1936b, 1938), McDunnough (1928, 1929), Shepard (1964), Skinner (1893, 1921), Stallings and Turner (1947), and Wright (1922). A manuscript checklist of Montana butterflies was prepared in 1941 by Thomas Rogers (Spokane, Washington) but was never published.

Elrod's "Butterflies of Montana," though an excellent treatment for its time, is now out-of-date. The nomenclature is antiquated, and the coverage mainly limited to a few counties where collections had been made at that time (Missoula, Flathead, Gallatin, Park, Custer, Lewis & Clark counties). There are also some errors in identification. Copies of the publication are almost impossible to obtain.

Thomas Rogers' manuscript checklist is also restricted in its coverage, listing mainly records from the northwestern part of the state and repeating many of the Elrod records. The nomenclature used is also out-of-date, and, since it was never published, the list has been available to only a very few people.

Montana is a large state; approximately 540 miles in length, with an average width of 275 miles. It is endowed with great variety of habitat and terrain as well as climate. The highest point is Granite Peak (12,799 ft.) in the Beartooth Range, Park Co. The lowest, 1,820 ft., is where Highway 2 crosses the Montana-Idaho border northwest of Troy in Lincoln Co. The western two-fifths of Montana are mountainous; the main Rocky Mountain chain runs north–south across the state. This western mountainous region has received the most attention in the past. The eastern three-fifths of the state are high, rolling prairie country, interrupted by several small mountain ranges. This region has been collected sporadically, and some counties do not have a single species recorded.

Data for county records were obtained from:

(1) The Elrod collection, University of Montana, Missoula. This also includes a collection made by G. E. Barnes in southern Park Co. and the C. A. Wiley collection from Miles City, Custer Co.

(2) The Montana State University collection, Bozeman. Early work on this collection was done by R. A. Cooley, R. E. Hutchins, E. Koch, and A. D. Hastings. The large collection of C. C. Albright, Great Falls, also came to Montana State University at his death, and another small collection by J. J. McDonald of Helena was donated at his death. Albright, a Great Falls physician, collected extensively in the Little Belt Mountains around Monarch, Cascade Co., where he had a summer home. McDonald collected in the vicinity of Helena and the Big Belt Mountains.

(3) The collection of Glacier National Park at park headquarters, West Glacier, which contains eight drawers of butterflies, mainly collected by J. S. Garth in the 1930's.

(4) Private collections of J. E. Crystal, Plains; F. E. Holley, Hamilton; J. Goosey, Jr., Big Timber; and my extensive collection.

(5) A review of the published literature.

(6) Montana collection records provided by non-resident collectors.
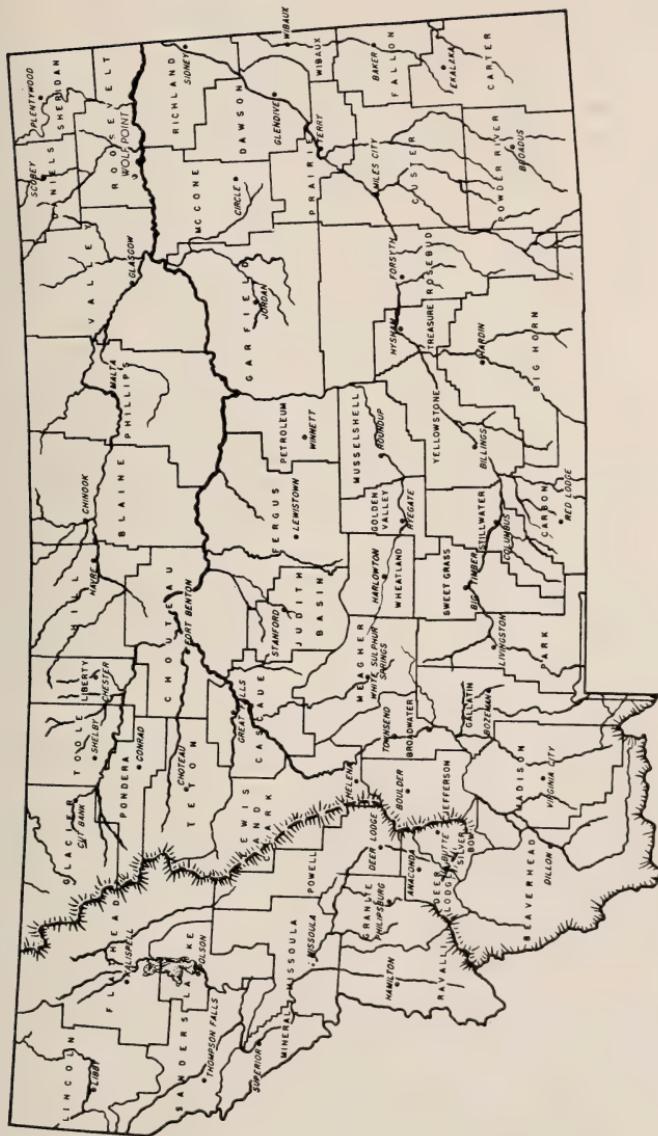
Fig. 1. Map of Montana showing county boundaries.

TABLE 1. Number of Montana butterfly species recorded by county.

Carbon	128	Dawson	29
Gallatin	115	Yellowstone	28
Flathead	113	Big Horn	27
Missoula	113	Blaine	27
Sweet Grass	102	Deer Lodge	23
Cascade	96	Musselshell	22
Lake	96	Prairie	19
Lewis & Clark	95	Rosebud	17
Madison	95	Fallon	15
Ravalli	87	Hill	13
Sanders	83	Teton	8
Glacier	78	Toole	8
Beaverhead	77	Powder River	7
Granite	71	Richland	7
Powell	71	Wibaux	7
Fergus	69	Valley	5
Mineral	67	Liberty	4
Custer	66	Pondera	4
Stillwater	66	Wheatland	4
Chouteau	63	Phillips	2
Lincoln	61	Roosevelt	2
Jefferson	60	Garfield	1
Park	60	Petroleum	1
Meagher	49	Sheridan	1
Judith Basin	36	Treasure	1
Broadwater	35	Carter	0
Silver Bow	35	Daniels	0
Golden Valley	33	McCone	0

(7) Information obtained from the major natural history museums. Unfortunately, there is considerable material in some of these museums that I have not yet examined. It is hoped that this task will be accomplished before the larger work is published. Museums that have collections containing substantial amounts of Montana material are: Allyn Museum of Entomology, Sarasota; American Museum of Natural History, New York; California Academy of Sciences, San Francisco; Canadian National Collection, Ottawa; Carnegie Museum, Pittsburgh; Los Angeles County Museum of Natural History, Los Angeles; Museum of Comparative Zoology, Harvard University, Cambridge; National Museum of Natural History, Washington, D. C.; Peabody Museum of Natural History, Yale University, New Haven; Texas Memorial Museum, Austin. I would certainly appreciate hearing from curators of collections in other institutions if they have Montana material.

Notes on several species are given in the checklist, especially if the nomenclature of the species is in question. Location of counties is

shown on the Montana map in Fig. 1. Table 1 shows the number of butterfly species recorded in each county.

COUNTY RECORDS OF MONTANA BUTTERFLIES

Megathymidae

Megathymus Scudder, 1872

1   *streckeri leussleri* Holland—Custer, Rosebud.

Hesperiidae

Amblyscirtes Scudder, 1872

2   *vialis* (W. H. Edwards)—Carbon, Flathead, Lake, Lincoln, Mineral, Missoula.

Euphyes Scudder, 1872

3   *vestris metacomet* (Harris)—Sweet Grass.

Ochlodes Scudder, 1872

4a   *sylvanoides sylvanoides* (Boisduval)—Flathead, Granite, Lake, Lewis & Clark, Lincoln, Mineral, Missoula, Ravalli, Sanders.
4b   *sylvanoides napa* (W. H. Edwards)—Broadwater, Carbon, Cascade, Chouteau, Gallatin, Golden Valley, Musselshell, Stillwater, Sweet Grass, Toole, Yellowstone.

Atrytone Scudder, 1872

5   *logan lagus* (W. H. Edwards)—Cascade, Custer, Powder River. The American Museum of Natural History has specimens labeled only "Montana" (Stanford, 1975).

Atalopedes Scudder, 1872

6   *campestris* (Boisduval)—Specimens are in the American Museum of Natural History which are labeled only "Montana" (Stanford, 1975).

Polites Scudder, 1872

7   *peckius* (Kirby)—Carbon, Gallatin, Lincoln, Missoula, Petroleum.
8   *sabuleti sabuleti* (Boisduval)—The American Museum of Natural History has two specimens labeled only "Montana" (Stanford, 1975).
9   *draco* (W. H. Edwards)—Beaverhead, Broadwater, Carbon, Chouteau, Fergus, Flathead, Gallatin, Glacier, Madison, Powell, Stillwater, Sweet Grass.
10   *themistocles* (Latreille)—Carbon, Cascade, Custer, Flathead, Gallatin, Lewis & Clark, Madison, Sweet Grass.
11   *origenes rhena* (W. H. Edwards)—Gallatin, Madison.
12   *mystic* ssp.—Carbon, Cascade, Chouteau, Gallatin, Lincoln, Mineral, Missoula, Stillwater, Sweet Grass. MacNeil (in Howe, 1975) feels that Montana, Idaho, Washington, and British Columbia *mystic* may represent an unnamed subspecies.
13   *sonora utahensis* (Skinner)—Carbon, Gallatin. There is a specimen from Lake View, Montana (no county given) in the U.S. National Museum, as well as additional specimens labeled only "Montana" (Stanford, 1975).

Hesperia Fabricius, 1793

14   *uncas uncas* W. H. Edwards—Beaverhead, Cascade, Chouteau, Fallon, Flathead, Gallatin, Golden Valley, Hill, Lake, Madison, Missoula, Toole.

15a *comma assiniboia* (Lyman)—Dawson.
15b *comma manitoba* (Scudder)—Carbon, Flathead, Lake, Lewis & Clark, Missoula, Park, Powell, Sweet Grass, Toole.
15c *comma harpalus* (W. H. Edwards)—Beaverhead, Broadwater, Carbon, Cascade, Chouteau, Gallatin, Golden Valley, Madison, Meagher, Missoula, Musselshell, Park, Ravalli, Stillwater, Sweet Grass, Yellowstone.
15d *comma oregonia* (W. H. Edwards)—Sanders.
15e *comma oregonia/harpalus*—Flathead, Glacier, Lake, Lincoln, Mineral. Specimens of *comma* from the northwestern part of the state appear to be blends of *oregonia* and *harpalus*.
16 *nevada* (Scudder)—Beaverhead, Carbon, Fergus, Gallatin, Glacier, Golden Valley, Jefferson, Lake, Lewis & Clark, Missoula, Musselshell, Ravalli, Sweet Grass, Yellowstone.
17 *pahaska pahaska* Leussler—Carbon, Cascade, Golden Valley, Yellowstone.
18 *juba* (Scudder)—Gallatin, Lake, Madison, Yellowstone.
19 *leonardus pawnee* Dodge—Big Horn, Chouteau, Custer, Dawson, Prairie. There are additional specimens collected by Dodge and Neumogen in the U.S. National Museum labeled only "Montana" (Stanford, 1975).
20 *ottoe* W. H. Edwards—Custer, Prairie. Additional specimens labeled only "Montana" are in the U.S. National Museum and the American Museum of Natural History (Stanford, 1975).

Oarisma Scudder, 1872

21 *garita garita* (Reakirt)—Carbon, Cascade, Chouteau, Custer, Flathead, Gallatin, Glacier, Golden Valley, Granite, Lewis & Clark, Lincoln, Madison, Mineral, Missoula, Powell, Ravalli, Richland, Sanders, Sweet Grass.

Carterocephalus Lederer, 1852

22 *palaemon mandan* (W. H. Edwards)—Beaverhead, Carbon, Cascade, Flathead, Gallatin, Glacier, Lake, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Sanders, Sweet Grass.

Pholisora Scudder, 1872

23 *catullus* (Fabricius)—Carbon, Cascade, Chouteau, Custer, Dawson, Gallatin, Lewis & Clark, Missoula, Ravalli, Sanders, Sweet Grass, Yellowstone.

Hesperopsis Dyar, 1905

24 *libya lena* (W. H. Edwards)—Custer, Dawson. Additional specimens labeled only "Montana" are in the collections of the U.S. National Museum, American Museum of Natural History and the Brooklyn Museum (Stanford, 1975; Field, 1976).

Pyrgus Hübner, 1816

25 *centaureae loki* Evans—Carbon, Flathead, Glacier, Lake, Lewis & Clark, Park.
26 *ruralis* (Boisduval)—Beaverhead, Carbon, Cascade, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Granite, Lake, Lewis & Clark, Lincoln, Madison, Missoula, Park, Ravalli, Sweet Grass.
27 *communis communis* (Grote)—Blaine, Broadwater, Carbon, Cascade, Chouteau, Custer, Dawson, Deer Lodge, Fallon, Flathead, Gallatin, Golden Valley, Jefferson, Lake, Lewis & Clark, Madison, Mineral, Missoula, Musselshell, Park, Prairie, Richland, Sanders.

Erynnis Schrank, 1801

28 *icelus* (Scudder & Burgess)—Carbon, Fergus, Flathead, Gallatin, Glacier, Jefferson, Lincoln, Madison, Mineral, Missoula, Ravalli, Roosevelt, Sanders, Sweet Grass.
29 *persius fredericki* H. A. Freeman—Beaverhead, Cascade, Chouteau, Fergus, Gal-

latin, Granite, Lake, Lewis & Clark, Meagher, Mineral, Missoula, Powell, Ravalli, Sanders, Silver Bow, Sweet Grass.

30 *afranius* (Lintner)—Beaverhead, Cascade, Fergus, Flathead, Gallatin, Glacier, Judith Basin, Lake, Lewis & Clark, Madison, Meagher, Missoula, Powell.

31 *pacuvius lilius* (Dyar)—Flathead, Gallatin, Lake, Sanders, Yellowstone.

Thorybes Scudder, 1872

32 *pylades pylades* (Scudder)—Cascade, Chouteau, Custer, Flathead, Gallatin, Jefferson, Lincoln, Sweet Grass, Yellowstone.

Epargyreus Hübner, 1816

33 *clarus clarus* (Cramer)—Big Horn, Carbon, Cascade, Chouteau, Custer, Flathead, Gallatin, Lake, Lewis & Clark, Lincoln, Missoula, Sanders, Sweet Grass.

Papilionidae

Parnassius Latreille, 1804

34 *clodius gallatinus* Stichel—Flathead, Gallatin, Glacier, Madison, Mineral, Missoula, Park, Ravalli. References to *altaurus* Dyar in Montana represent *gallatinus*. Ferris (1976b) restricts the range of *altaurus* to Blaine and Custer counties, Idaho.

35a *phoebus smintheus* Doubleday—Glacier. Ferris (1976a) treated *xanthus* Ehrmann and *idahoensis* Bryk & Eisner, both of which have been referred to Montana, as synonyms of *smintheus*.

35b *phoebus montanulus* Bryk & Eisner—Beaverhead, Carbon, Cascade, Chouteau, Fergus, Flathead, Gallatin, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sanders, Stillwater, Sweet Grass, Teton. Ferris (1976a) has treated *maximus* Bryk & Eisner as a synonym of *montanulus*. His arrangement for both *smintheus* and *montanulus* seems logical and is followed here, although *maximus* (TL Judith Mountains, Fergus Co.), because of the large size and melanic appearance of the females, may be distinct enough to be considered a separate subspecies.

Papilio Linnaeus, 1758

36 *polyxenes asterius* Stoll—Sweet Grass. One specimen, a female, is in the collection of John Goosey, Jr., Big Timber.

37 *bairdii* f. "brucei" W. H. Edwards—Carbon, Cascade, Custer, Gallatin, Lewis & Clark, Madison, Musselshell, Prairie. The taxonomic status of *bairdii* W. H. Edwards, "brucei," and *oregonius* W. H. Edwards is still not completely resolved. Emmel's arrangement in Howe (1975) is followed.

38 *oregonius* W. H. Edwards—Lake, Missoula, Sanders.

39a *zelicaon nitra* W. H. Edwards—Cascade, Fergus, Glacier, Golden Valley, Granite, Meagher, Missoula, Powell, Sanders. Fisher's (1977) paper outlining his breeding experiments has clarified the relationship of *nitra*, *zelicaon* Lucas and "gothica" Remington. His proposed arrangement is followed here.

39b *zelicaon nitra* f. norm. "gothica"—Beaverhead, Carbon, Cascade, Chouteau, Custer, Deer Lodge, Fallon, Fergus, Flathead, Gallatin, Golden Valley, Granite, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sanders, Sweet Grass. This is the much more abundant, yellow "normal form" of *nitra*.

40 *indra indra* Reakirt—Carbon, Gallatin, Lewis & Clark.

41 *glaucus canadensis* Rothschild & Jordan—Carbon, Cascade, Custer, Flathead, Glacier, Judith Basin, Lincoln, Sanders. Elrod (1906) reports several specimens in Wiley's Miles City collection. Since Elrod outlines the differences between *glaucus* and *rutulus* Lucas in his discussion, I feel that these specimens were in

fact *glaucus* and not *rutulus*. The specimens could not be located in the remnants of the Elrod collection.

42 *rutulus rutulus* Lucas—Beaverhead, Big Horn, Carbon, Deer Lodge, Flathead, Gallatin, Glacier, Jefferson, Lake, Lewis & Clark, Lincoln, Madison, Mineral, Missoula, Park, Powell, Sanders, Sweet Grass.

43 *multicaudatus* Kirby—Beaverhead, Cascade, Flathead, Gallatin, Jefferson, Lake, Lewis & Clark, Madison, Mineral, Missoula, Pondera, Powell, Ravalli, Rosebud, Sanders, Sweet Grass.

44 *eurymedon* Lucas—Big Horn, Carbon, Cascade, Custer, Flathead, Gallatin, Granite, Jefferson, Lake, Lewis & Clark, Madison, Mineral, Missoula, Powell, Ravalli, Sanders, Sweet Grass.

Pieridae

Neophasia Behr, 1869

45a *menapia menapia* (Felder & Felder)—Carbon, Fergus.

45b *menapia* nr. *tau* (Scudder)—Broadwater, Flathead, Granite, Jefferson, Lake, Lewis & Clark, Lincoln, Mineral, Missoula, Powell, Ravalli, Sanders, Silver Bow.

Pieris Schrank, 1801

46 *beckerii* W. H. Edwards—Beaverhead, Broadwater, Carbon, Flathead, Gallatin, Granite, Jefferson, Lake, Lewis & Clark, Madison, Mineral, Missoula, Park, Sanders, Sweet Grass, Wheatland.

47 *sisymbrii elivata* (Barnes & Benjamin)—Beaverhead, Flathead, Gallatin, Granite, Jefferson, Lake, Madison, Missoula, Powell, Ravalli, Sanders.

48 *protodice* Boisduval & LeConte—Beaverhead, Carbon, Cascade, Chouteau, Custer, Deer Lodge, Flathead, Gallatin, Golden Valley, Granite, Lake, Lewis & Clark, Madison, Missoula, Park, Yellowstone. Shapiro's (1976) arrangement of the *protodice-occidentalis* group is followed.

49 *occidentalis occidentalis* Reakirt—Beaverhead, Blaine, Broadwater, Carbon, Cascade, Chouteau, Custer, Dawson, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Ravalli, Sanders, Stillwater, Sweet Grass, Teton, Yellowstone.

50 *napi macdunnoughii* Remington—Beaverhead, Big Horn, Carbon, Cascade, Chouteau, Custer, Fergus, Flathead, Gallatin, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sanders, Stillwater, Sweet Grass.

51 *rapae* (Linnaeus)—Beaverhead, Big Horn, Blaine, Broadwater, Carbon, Cascade, Chouteau, Custer, Flathead, Gallatin, Granite, Lake, Lewis & Clark, Madison, Meagher, Mineral, Missoula, Park, Ravalli, Sanders, Stillwater, Sweet Grass, Yellowstone.

Colias Fabricius, 1807

52a *meadii meadii* W. H. Edwards—Carbon, Gallatin, Madison, Park, Stillwater, Sweet Grass.

52b *meadii elis* Strecker—Flathead, Glacier.

53 *eurytheme* Boisduval—Cascade, Custer, Flathead, Gallatin, Glacier, Granite, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Musselshell, Ravalli, Sanders, Sweet Grass.

54 *philodice philodice* Godart—Beaverhead, Big Horn, Blaine, Broadwater, Carbon, Cascade, Chouteau, Custer, Dawson, Deer Lodge, Fallon, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Musselshell, Park, Pondera, Powder River, Powell, Ravalli, Rosebud, Sanders, Silver Bow, Still-

water, Sweet Grass, Teton, Valley, Wibaux, Yellowstone. Included here is *eriphyle* W. H. Edwards.

55 *interior interior* Scudder—Flathead, Gallatin, Granite, Jefferson, Lake, Lewis & Clark, Lincoln, Madison, Mineral, Missoula, Ravalli, Sanders.

56 *gigantea harroweri* Klots—Gallatin.

57a *alexandra columbiensis* Ferris—Flathead, Lake, Lincoln, Mineral, Missoula, Ravalli, Sanders. Many specimens show characters associated with both *columbiensis* and *astraea* W. H. Edwards (Ferris, 1973).

57b *alexandra astraea* W. H. Edwards—Beaverhead, Carbon, Cascade, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Jefferson, Lake, Lewis & Clark, Madison, Meagher, Park, Powell, Ravalli, Silver Bow, Stillwater, Sweet Grass, Toole. Male specimens grouped here under *astraea* show a great deal of variation and are mixed orange to yellow populations. Females are white.

58 *pelidne skinneri* Barnes—Beaverhead, Carbon, Cascade, Gallatin, Glacier, Granite, Jefferson, Lewis & Clark, Meagher, Missoula, Powell, Ravalli, Stillwater, Sweet Grass.

59 *nastes streckeri* Grum-Grshmaïlo—Flathead, Glacier.

Phoebis Hübner, 1816

60 *sennae eubule* (Linnaeus)—Carbon.

Nathalis Boisduval, 1836

61 *iole* Boisduval—Missoula, Stillwater. There is no breeding population of *iole* in Montana. The captures surely are migrants.

Anthocharis Boisduval, Rambur & Graslin, 1833

62 *sara julia* W. H. Edwards—Beaverhead, Broadwater, Carbon, Cascade, Deer Lodge, Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Lake, Lewis & Clark, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sanders, Silver Bow, Stillwater, Sweet Grass.

Euchloe Hübner, 1816

63 *ausonides coloradensis* (H. Edwards)—Beaverhead, Big Horn, Carbon, Cascade, Chouteau, Deer Lodge, Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sanders, Silver Bow, Sweet Grass. Some authors consider *coloradensis* a synonym of *ausonides* Lucas (Howe, 1975). California and western mountain populations differ from Rocky Mountain populations in the appearance of the females. The name *coloradensis* is used here for Montana specimens, and *ausonides* is restricted to the more western populations.

64 *olympia* f. "rosa" (W. H. Edwards)—Cascade, Custer, Fallon, Fergus, Gallatin, Golden Valley, Hill, Musselshell, Park, Prairie, Sweet Grass. "rosa" is best considered a form rather than a subspecies.

65 *hyantis hyantis* (W. H. Edwards)—Broadwater, Granite, Jefferson, Madison, Ravalli, Sanders.

Riodinidae

Apodemia Felder & Felder, 1865

66 *mormo mormo* (Felder & Felder)—Prairie, Valley.

Lycaenidae

Harkenclenus dos Passos, 1970

67a *titus titus* (Fabricius)—Dawson.

67b   *titus immaculosus* (Comstock)—Carbon, Cascade, Chouteau, Fergus, Flathead, Glacier, Lewis & Clark, Madison, Mineral, Missoula, Ravalli, Stillwater, Sweet Grass.

Satyrium Scudder, 1876

68   *fuliginosum semiluna* Klots—Big Horn, Carbon, Gallatin, Meagher, Sweet Grass, Wheatland.

69   *saepium okanagana* (McDunnough)—Carbon, Cascade, Flathead, Jefferson, Lake, Mineral, Missoula, Ravalli, Sanders, Stillwater.

70   *liparops aliparops* (Michener & dos Passos)—Dawson, Prairie, Stillwater, Sweet Grass.

71   *sylvinus* ssp.—Carbon, Cascade, Flathead, Jefferson, Lake, Madison, Mineral, Missoula, Ravalli, Sanders. *S. californica* (W. H. Edwards) has been reported from Montana on several occasions. I have not been able to examine all the specimens, but those I have seen appear to be *sylvinus*. For the present, all records for *californica* have been included here. There are no native *Quercus* (oak) in Montana, which is the reported larval food of *californica*, while *Salix* (willow), the food of *sylvinus* is widely distributed.

72   *acadica montanensis* (Watson & Comstock)—Carbon, Custer, Sweet Grass.

Callophrys Billberg, 1820

73   *polios obscurus* Ferris & Fisher—Carbon, Cascade, Custer, Fergus, Flathead, Golden Valley, Granite, Lake, Lewis & Clark, Mineral, Missoula, Ravalli, Sanders, Silver Bow.

74   *mossii schryveri* (Cross)—Granite, Lake, Mineral, Missoula, Ravalli, Sanders, Silver Bow.

75   *augustinus iroides* (Boisduval)—Carbon, Fergus, Flathead, Gallatin, Granite, Lake, Lewis & Clark, Mineral, Missoula, Park, Powell, Ravalli, Sanders.

76   *eryphon eryphon* (Boisduval)—Beaverhead, Carbon, Cascade, Custer, Fergus, Flathead, Gallatin, Glacier, Granite, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Powell, Ravalli, Sanders, Silver Bow, Stillwater, Sweet Grass. Elrod (1906) made reference to two records (Miles City, Custer Co. and Bozeman, Gallatin Co.) for *niphon* (Hübner). These records are considered doubtful, and the specimens could not be located. For the present, *niphon* should not be considered as occurring in Montana.

77   *spinetorum* (Hewitson)—Beaverhead, Carbon, Cascade, Fergus, Flathead, Gallatin, Glacier, Granite, Judith Basin, Lake, Lewis & Clark, Lincoln, Missoula, Powell, Ravalli, Sanders.

78   *siva siva* (W. H. Edwards)—Big Horn, Broadwater, Cascade, Custer, Dawson, Deer Lodge, Fallon, Gallatin, Granite, Jefferson, Lake, Lewis & Clark, Madison, Missoula, Park, Powell, Rosebud, Sanders, Silver Bow, Stillwater, Sweet Grass, Yellowstone.

79   *byrnei* Johnson—Ravalli, Sanders. Johnson (1976) has split the *nelsoni* (Boisduval) complex into four different species. Montana specimens from near Noxon, Sanders Co., were taken closest geographically to the range he outlines for *byrnei*, though he studied no Montana specimens. Johnson's study was based on relatively few specimens. It remains to be seen if his is the best approach to the *nelsoni* complex, but his treatment will be followed for the present. Montana specimens may also represent his *rosneri*, though too few are available to place them accurately.

80   *affinis affinis* (W. H. Edwards)—Carbon, Fergus, Gallatin, Lewis & Clark, Madison, Missoula, Sweet Grass.

81   *sheridanii* nr. *neoperplexa* (Barnes & Benjamin)—Beaverhead, Big Horn, Carbon, Gallatin, Granite, Jefferson, Madison, Powell, Ravalli, Sanders, Silver Bow. Specimens are intermediate between *neoperplexa* and *sheridanii* (W. H. Edwards), but appear to be closer to *neoperplexa*.

Strymon Hübner, 1818

82 *melinus setonia* McDunnough—Big Horn, Carbon, Custer, Dawson, Deer Lodge, Fallon, Fergus, Flathead, Jefferson, Lake, Lewis & Clark, Mineral, Missoula, Ravalli, Rosebud, Sanders, Silver Bow, Stillwater, Sweet Grass, Yellowstone.

Lycaena Fabricius, 1807

83a *phlaeas americana* Harris—Custer. This subspecies is included on the basis of specimens from Miles City reported by Wiley (Elrod, 1906) These specimens could not be located.

83b *phlaeas arethusa* (Wolley-Dod)—Flathead, Glacier.

83c *phlaeas arctodon* Ferris—Carbon, Judith Basin, Sweet Grass.

84 *cupreus snowi* (W. H. Edwards)—Beaverhead, Carbon, Cascade, Fergus, Flathead, Gallatin, Glacier, Lake, Madison, Park, Sweet Grass. Miller and Brown (1979) retain only *phlaeas* and *cupreus* in *Lycaena*. The other species formerly listed in *Lycaena* have been placed by them in the genera which follow. Their entire arrangement is used here.

Gaeides Scudder, 1876

85 *xanthoides dione* (Scudder)—Carbon, Cascade, Chouteau, Custer, Dawson, Glacier, Lewis & Clark, Prairie, Stillwater, Sweet Grass.

86 *editha montana* (Field)—Beaverhead, Broadwater, Carbon, Cascade, Chouteau, Flathead, Gallatin, Granite, Jefferson, Lake, Lewis & Clark, Madison, Mineral, Missoula, Ravalli, Stillwater, Sweet Grass.

Hyllolycaena L. Miller & F. M. Brown, 1979

87 *hyllus* (Cramer)—Garfield, Prairie. This species was previously known as *thoe* Guérin-Méneville until Brown and Field (1970) showed the correct name as *hyllus*.

Chalceria Scudder, 1876

88a *rubidus sirius* (W. H. Edwards)—Blaine, Cascade, Custer, Flathead, Hill, Lake, Liberty, Powder River.

88b *rubidus duofacies* (Johnson & Balogh)—Beaverhead, Carbon, Gallatin, Lewis & Clark, Madison, Park, Powell, Silver Bow, Sweet Grass. This subspecies was only recently described (Johnson & Balogh, 1977).

89 *heteronea klotsi* (Field)—Beaverhead, Broadwater, Carbon, Cascade, Flathead, Gallatin, Glacier, Lake, Lewis & Clark, Madison, Missoula, Powell, Ravalli, Silver Bow, Stillwater, Sweet Grass.

Epidemia Scudder, 1876

90 *helloides* (Boisduval)—Beaverhead, Carbon, Cascade, Chouteau, Custer, Flathead, Gallatin, Jefferson, Judith Basin, Lake, Lewis & Clark, Liberty, Madison, Meagher, Missoula, Park, Prairie, Sanders, Stillwater, Sweet Grass, Toole. Ferris (1977) has clarified the relationship of *helloides* and *dorcas* (Kirby).

91 *dorcas florus* (W. H. Edwards)—Beaverhead, Broadwater, Carbon, Cascade, Chouteau, Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Lake, Lewis & Clark, Madison, Meagher, Missoula, Park, Ravalli, Sanders, Stillwater, Sweet Grass.

92 *mariposa penroseae* (Field)—Carbon, Cascade, Flathead, Gallatin, Glacier, Granite, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Powell, Ravalli, Sanders, Stillwater.

93 *nivalis browni* (dos Passos)—Beaverhead, Carbon, Flathead, Glacier, Mineral, Missoula, Ravalli.

Lycaeides Hübner, 1816

94a *argyrognomon atrapraetextus* (Field)—Beaverhead, Cascade, Deer Lodge, Flat-

head, Glacier, Granite, Lake, Lincoln, Mineral, Missoula, Powell, Ravalli, Sanders.

94b *argyrognomon longinus* Nabokov—Carbon, Gallatin, Jefferson, Stillwater.

95 *melissa melissa* (W. H. Edwards)—Beaverhead, Blaine, Broadwater, Carbon, Cascade, Chouteau, Custer, Dawson, Deer Lodge, Fallon, Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Madison, Meagher, Missoula, Musselshell, Park, Powell, Prairie, Ravalli, Richland, Sheridan, Stillwater, Sweet Grass, Teton, Wibaux, Yellowstone.

Plebejus Kluk, 1802

96 *saepiolus saepiolus* (Boisduval)—Beaverhead, Big Horn, Broadwater, Carbon, Cascade, Chouteau, Custer, Deer Lodge, Fallon, Fergus, Flathead, Gallatin, Glacier, Judith Basin, Lake, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Richland, Sanders, Silver Bow, Stillwater, Sweet Grass, Wibaux.

97a *icarioides lycea* (W. H. Edwards)—Beaverhead, Big Horn, Broadwater, Carbon, Cascade, Chouteau, Custer, Deer Lodge, Fallon, Fergus, Gallatin, Jefferson, Madison, Meagher, Park, Silver Bow, Stillwater, Sweet Grass, Yellowstone.

97b *icarioides pembina* (W. H. Edwards)—Beaverhead, Big Horn, Fallon, Flathead, Glacier, Granite, Lake, Lewis & Clark, Lincoln, Mineral, Missoula, Powell, Ravalli, Sanders.

98 *shasta minnehaha* (Scudder)—Carbon, Fergus, Meagher, Richland, Sweet Grass.

99 *acmon lutzi* dos Passos—Carbon, Deer Lodge, Gallatin, Golden Valley, Lewis & Clark, Lincoln, Madison, Missoula, Park, Ravalli, Sanders, Stillwater, Sweet Grass.

100a *glandon megalo* McDunnough—Blaine, Cascade, Chouteau, Fergus, Flathead, Glacier, Granite, Judith Basin, Lewis & Clark, Lincoln, Missoula, Powell.

100b *glandon rustica* (W. H. Edwards)—Beaverhead, Carbon, Deer Lodge, Gallatin, Madison, Park, Stillwater, Sweet Grass.

Everes Hübner, 1816

101 *amyntula albrighti* Clench—Blaine, Broadwater, Carbon, Cascade, Chouteau, Fergus, Flathead, Gallatin, Glacier, Jefferson, Lake, Lincoln, Madison, Missoula, Park, Pondera, Powell, Ravalli, Sanders, Sweet Grass, Teton.

Euphilotes Mattoni, 1977

102 *battoides glaucon* (W. H. Edwards)—Madison, Missoula, Ravalli. Shields (1975) discusses placing *battoides* and *enoptes* (Boisduval) in *Pseudophilotes* Beuret, an arrangement followed by several authors including Brown (1972), but retains them in *Shijimiaeoides* Beuret. Mattoni (1977) more recently erected a new genus, *Euphilotes*.

103 *enoptes ancilla* (Barnes & McDunnough)—Carbon, Gallatin, Madison, Missoula, Ravalli, Sweet Grass.

Glaucopsyche Scudder, 1872

104 *lygdamus oro* Scudder—Beaverhead, Big Horn, Broadwater, Carbon, Custer, Deer Lodge, Fallon, Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Mineral, Missoula, Musselshell, Park, Powell, Ravalli, Rosebud, Sanders, Silver Bow, Stillwater, Sweet Grass, Wibaux, Yellowstone. There is blending with *columbia* Skinner in the northwestern counties.

105 *piasus daunia* W. H. Edwards—Beaverhead, Big Horn, Carbon, Cascade, Deer Lodge, Fergus, Flathead, Gallatin, Glacier, Granite, Lewis & Clark, Lincoln, Madison, Missoula, Powell, Sanders, Silver Bow, Sweet Grass.

Celastrina Tutt, 1906

106 *argiolus pseudargiolus* (Boisduval & LeConte)—Big Horn, Carbon, Chouteau,

Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Lake, Lewis & Clark, Mineral, Missoula, Ravalli, Sanders, Sweet Grass.

Nymphalidae

Limenitis Fabricius, 1807

107 *arthemis rubrofasciata* (Barnes & McDunnough)—Flathead, Glacier.
108 *archippus archippus* (Cramer)—Carbon, Chouteau, Custer, Gallatin, Granite, Lake, Madison, Missoula, Park, Powell, Ravalli, Sweet Grass, Yellowstone.
109a *weidemeyerii latifascia* Perkins & Perkins—Beaverhead, Carbon, Cascade, Chouteau, Fergus, Flathead, Gallatin, Granite, Lewis & Clark, Madison, Mineral, Powell, Ravalli, Silver Bow, Stillwater, Sweet Grass.
109b *weidemeyerii oberfoelli* Brown—Custer, Dawson, Prairie.
110 *lorquini burrisonii* Maynard—Beaverhead, Flathead, Glacier, Granite, Lake, Lewis & Clark, Lincoln, Mineral, Missoula, Powell, Ravalli, Sanders.

Vanessa Fabricius, 1807

111 *atalanta rubria* (Fruhstorfer)—Beaverhead, Carbon, Cascade, Chouteau, Dawson, Fergus, Flathead, Gallatin, Golden Valley, Judith Basin, Lake, Lewis & Clark, Liberty, Lincoln, Madison, Missoula, Powell, Sanders, Sweet Grass.
112 *virginiensis* (Drury)—Carbon.
113 *cardui* (Linnaeus)—Beaverhead, Broadwater, Carbon, Cascade, Chouteau, Custer, Deer Lodge, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Granite, Jefferson, Lake, Lewis & Clark, Lincoln, Madison, Mineral, Missoula, Musselshell, Powell, Ravalli, Rosebud, Sanders, Silver Bow, Stillwater, Sweet Grass, Teton.
114 *annabella* (Field)—Beaverhead, Carbon, Cascade, Custer, Flathead, Gallatin, Granite, Lake, Madison, Missoula, Ravalli, Sanders.

Nymphalis Kluk, 1802

115 *vau-album watsoni* (Hall)—Carbon, Custer, Flathead, Gallatin, Glacier, Lake, Mineral, Missoula, Ravalli, Sanders, Sweet Grass.
116 *californica herri* Field—Carbon, Custer, Flathead, Gallatin, Granite, Lake, Lewis & Clark, Lincoln, Madison, Mineral, Missoula, Powell, Ravalli, Sanders.
117 *milberti furcillata* (Say)—Beaverhead, Big Horn, Blaine, Carbon, Cascade, Chouteau, Custer, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Granite, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Musselshell, Park, Powell, Prairie, Ravalli, Sanders, Silver Bow, Stillwater, Sweet Grass.
118 *antiopa antiopa* (Linnaeus)—Carbon, Cascade, Chouteau, Custer, Fergus, Flathead, Gallatin, Glacier, Granite, Hill, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Missoula, Musselshell, Ravalli, Sanders, Silver Bow, Stillwater, Sweet Grass.

Polygonia Hübner, 1816

119 *satyrus satyrus* (W. H. Edwards)—Beaverhead, Carbon, Cascade, Chouteau, Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Lake, Lewis & Clark, Lincoln, Madison, Missoula, Park, Powell, Ravalli, Sanders, Silver Bow, Stillwater, Sweet Grass.
120 *faunus rusticus* (W. H. Edwards)—Carbon, Cascade, Fergus, Flathead, Gallatin, Glacier, Granite, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Ravalli, Sanders, Silver Bow, Stillwater, Sweet Grass.
121 *zephyrus* (W. H. Edwards)—Beaverhead, Blaine, Broadwater, Carbon, Cascade, Chouteau, Custer, Fergus, Flathead, Gallatin, Glacier, Granite, Judith Basin, Lake, Lewis & Clark, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Silver Bow, Stillwater, Sweet Grass.

122   *oreas silenus* (W. H. Edwards)—Carbon, Cascade, Flathead, Lake, Missoula, Park, Sanders, Sweet Grass. The Carbon, Park and Sweet Grass County records may be doubtful. I have not seen the specimens.
123   *progne* (Cramer)—Carbon. This also may be a doubtful record, but is retained for the present, until the specimen can be examined.

Charidryas Scudder, 1872

124   *nycteis drusius* (W. H. Edwards)—Carbon.
125   *gorgone carlotta* (Reakirt)—Cascade, Custer, Dawson, Fallon, Fergus, Gallatin, Phillips, Prairie, Richland, Rosebud, Stillwater, Wibaux, Yellowstone.
126   *acastus acastus* (W. H. Edwards)—Cascade, Custer, Dawson, Fallon, Flathead, Gallatin, Lewis & Clark, Prairie.
127   *damoetas damoetas* (Skinner)—Carbon, Flathead, Glacier.
128   *palla calydon* (Holland)—Broadwater, Carbon, Cascade, Chouteau, Custer, Fergus, Flathead, Gallatin, Glacier, Jefferson, Lake, Lewis & Clark, Lincoln, Madison, Mineral, Missoula, Powell, Ravalli, Sanders, Stillwater, Sweet Grass. Some Montana material is near *sterope* (W. H. Edwards).

Phyciodes Hübner, 1816

129   *tharos* ssp.—Beaverhead, Blaine, Broadwater, Carbon, Chouteau, Custer, Dawson, Fergus, Flathead, Gallatin, Glacier, Granite, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Musselshell, Powell, Prairie, Ravalli, Rosebud, Sanders, Stillwater, Sweet Grass.
130   *campestris campestris* (Behr)—Beaverhead, Blaine, Broadwater, Carbon, Cascade, Chouteau, Custer, Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Rosebud, Sanders, Stillwater, Sweet Grass, Yellowstone. There may be blending with *camillus* (W. H. Edwards) in the southwestern part of the state.
131   *mylitta mylitta* (W. H. Edwards)—Beaverhead, Big Horn, Blaine, Chouteau, Flathead, Gallatin, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Missoula, Powell, Ravalli, Sanders, Silver Bow, Sweet Grass.
132   *pallida barnesi* Skinner—Chouteau, Gallatin, Madison, Ravalli, Sweet Grass.

Hypodryas Higgins, 1978

133   *gillettii* (Barnes)—Beaverhead, Cascade, Fergus, Glacier, Golden Valley, Judith Basin, Madison, Mineral, Missoula, Sanders. Higgins (1978) has revised the genus *Euphydryas* Scudder, and erected two new genera for the North American species. He retained only *phaeton* (Drury), which does not occur in Montana, in the genus *Euphydryas*. His arrangement is followed here, though some may prefer to consider his new names as subgeneric, rather than generic.

Occidryas Higgins, 1978

134   *colon wallacensis* (Gunder)—Beaverhead, Flathead, Lake, Lewis & Clark, Lincoln, Mineral, Missoula, Powell, Ravalli, Sanders.
135a   *anicia anicia* (Doubleday)—Flathead, Glacier, Lake, Lincoln, Mineral, Sanders.
135b   *anicia howlandi* (Stallings & Turner)—Beaverhead, Gallatin, Jefferson, Lewis & Clark, Madison, Missoula, Ravalli.
135c   *anicia bernadetta* (Leussler)—Big Horn, Carbon, Cascade, Chouteau, Custer, Fergus, Meagher, Rosebud, Stillwater, Sweet Grass.
136a   *editha hutchinsi* (McDunnough)—Beaverhead, Broadwater, Carbon, Cascade, Flathead, Gallatin, Glacier, Golden Valley, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sweet Grass. Form "montanus" (McDunnough) occurs in the high mountains of the Beartooth Plateau in Carbon and Park counties.
136b   *editha* nr. *beani* (Skinner)—Flathead.

Boloria Moore, 1900

137a *selene tollandensis* (Barnes & Benjamin)—Beaverhead.
137b *selene atrocostalis/tollandensis*—Beaverhead, Carbon, Cascade, Chouteau, Custer, Dawson, Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Lake, Lewis & Clark, Lincoln, Madison, Missoula, Park, Powell, Ravalli, Silver Bow, Sweet Grass. Almost all of Montana, with the exception of a small portion of Beaverhead Co., falls within a broad blend zone of *atrocostalis* (Huard) and *tollandensis* (Kohler, 1977). Material from Custer and Dawson counties may prove to be *sabulocollis* Kohler, but I have not been able to examine the specimens.
138 *bellona* nr. *jenistai* Stallings & Turner—Fergus, Flathead, Lake, Lewis & Clark, Missoula. Montana representatives of *bellona* are in need of further study.
139 *kriemhild* (Strecker)—Carbon, Gallatin, Sweet Grass.
140 *epithore borealis* Perkins—Beaverhead, Flathead, Glacier, Granite, Hill, Lake, Lewis & Clark, Lincoln, Mineral, Missoula, Powell, Ravalli, Sanders, Silver Bow.
141 *freija browni* Higgins—Carbon.
142 *alberta* (W. H. Edwards)—Flathead, Glacier.
143 *astarte astarte* (Doubleday)—Flathead, Glacier.
144 *titania* ssp.—Carbon, Cascade, Flathead, Gallatin, Judith Basin, Madison, Meagher, Missoula, Park, Stillwater, Sweet Grass. The name *ingens* (Barnes & McDunnough) has been applied to Montana *titania*, but specimens do not compare well with Wyoming material. Possibly two unnamed subspecies of *titania* are present in Montana. The species is currently under study by Lee D. Miller.
145 *eunomia ursadentis* Ferris & Groothuis—Carbon, Stillwater.

Speyeria Scudder, 1872

146 *idalia* (Drury)—Custer. So far, only a single specimen has been taken, a female at Miles City by Wiley in 1893.
147 *edwardsii* (Reakirt)—Blaine, Carbon, Cascade, Chouteau, Custer, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Granite, Jefferson, Judith Basin, Lewis & Clark, Madison, Meagher, Missoula, Musselshell, Park, Powder River, Powell, Rosebud, Sanders, Stillwater, Sweet Grass, Valley.
148 *coronis* ssp.—Beaverhead, Carbon, Cascade, Chouteau, Custer, Deer Lodge, Fergus, Golden Valley, Jefferson, Lewis & Clark, Madison, Meagher, Musselshell, Powder River, Powell, Stillwater, Sweet Grass, Yellowstone. The name *halcyone* (W. H. Edwards) has usually been applied to Montana *coronis*, but Grey (1979) feels they would be better referred to as *snyderi* (Skinner). Most Montana *coronis* are greenish in the ventral hind wing discal area as in *snyderi*, rather than brownish like *halcyone*.
149 *zerene garretti* (Gunder)—Beaverhead, Big Horn, Blaine, Broadwater, Carbon, Cascade, Chouteau, Deer Lodge, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Granite, Hill, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Musselshell, Park, Powell, Ravalli, Sanders, Silver Bow, Stillwater, Sweet Grass, Wheatland.
150a *callippe gallatini* (McDunnough)—Beaverhead, Broadwater, Carbon, Cascade, Gallatin, Jefferson, Lewis & Clark, Madison, Meagher, Missoula, Park, Powell, Ravalli, Silver Bow, Stillwater, Sweet Grass.
150b *callippe calgariana* (McDunnough)—Blaine, Chouteau, Custer, Dawson, Fergus, Flathead, Glacier, Golden Valley, Lake, Liberty, Sanders, Teton, Valley. There is considerable blending of *gallatini* and *calgariana* characters over much of the state.
151a *egleis macdunnoughi* (Gunder)—Beaverhead, Gallatin, Park, Stillwater.
151b *egleis albrighti* (Gunder)—Carbon, Cascade, Chouteau, Fergus, Golden Valley, Lewis & Clark, Meagher, Sweet Grass.

151c *egleis* ssp.—Flathead, Glacier, Granite, Lake, Missoula, Powell, Ravalli.
152 *atlantis* ssp.—Beaverhead, Big Horn, Blaine, Carbon, Cascade, Chouteau, Custer, Fergus, Flathead, Gallatin, Glacier, Granite, Hill, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sanders, Stillwater, Sweet Grass, Toole. There is considerable variation in *atlantis* across the state. The name *hutchinsi* (Gunder) is conventionally applied to most material, but specimens approaching *beani* (Barnes & Benjamin) and *helena* dos Passos & Grey are often found in the variation (Grey, 1979).
153 *hydaspe sakuntala* (Skinner)—Beaverhead, Carbon, Cascade, Chouteau, Fergus, Flathead, Gallatin, Glacier, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sanders, Stillwater, Sweet Grass, Toole.
154 *mormonia eurynome* (W. H. Edwards)—Beaverhead, Big Horn, Blaine, Broadwater, Carbon, Cascade, Chouteau, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Granite, Hill, Jefferson, Judith Basin, Lake, Lewis & Clark, Madison, Meagher, Missoula, Park, Powell, Ravalli, Silver Bow, Stillwater, Sweet Grass, Teton, Wheatland.
155 *cybele leto* (Behr)—Beaverhead, Big Horn, Blaine, Carbon, Cascade, Chouteau, Custer, Dawson, Fergus, Flathead, Gallatin, Glacier, Granite, Hill, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sanders, Sweet Grass. Custer and Dawson County material may be closer to nominate *cybele* (Fabricius), but I have not been able to examine specimens.
156a *aphrodite manitoba* (Chermock & Chermock)—Big Horn, Custer, Dawson, Musselshell, Rosebud.
156b *aphrodite columbia* (H. Edwards)—Flathead, Lake, Lincoln, Missoula.
156c *aphrodite ethne* (Hemming)—Beaverhead, Blaine, Carbon, Cascade, Chouteau, Fergus, Gallatin, Golden Valley, Hill, Jefferson, Madison, Meagher, Park, Stillwater, Sweet Grass, Treasure. There is considerable intergrading of characters of the different subspecies of *aphrodite* in several areas.

Euptoieta Doubleday, 1848

157 *claudia* (Cramer)—Blaine, Carbon, Custer, Dawson, Fergus, Gallatin, Golden Valley, Hill, Madison, Prairie, Richland, Rosebud, Stillwater, Sweet Grass, Yellowstone.

Danaidae

Danaus Kluk, 1802

158 *plexippus plexippus* (Linnaeus)—Carbon, Cascade, Custer, Gallatin, Jefferson, Lake, Lewis & Clark, Madison, Missoula, Musselshell, Sanders, Sweet Grass.

Satyridae

Coenonympha Hübner, 1816

159a *ampelos ampelos* W. H. Edwards—Cascade, Flathead, Granite, Lake, Lincoln, Mineral, Missoula, Ravalli, Sanders.
159b *ampelos sweadneri* Chermock & Chermock—Mineral, Missoula.
160 *ochracea ochracea* W. H. Edwards—Beaverhead, Big Horn, Blaine, Broadwater, Carbon, Cascade, Chouteau, Custer, Fergus, Flathead, Gallatin, Granite, Jefferson, Lewis & Clark, Madison, Missoula, Park, Powell, Rosebud, Silver Bow, Stillwater, Sweet Grass, Yellowstone.
161 *inornata benjamini* McDunnough—Beaverhead, Blaine, Carbon, Cascade, Chouteau, Custer, Dawson, Fallon, Flathead, Gallatin, Glacier, Granite, Lake,

Lewis & Clark, Madison, Missoula, Pondera, Roosevelt, Rosebud, Stillwater, Toole, Wibaux, Yellowstone.

162   *haydenii* (W. H. Edwards)—Broadwater, Carbon, Cascade, Gallatin, Jefferson, Judith Basin, Lewis & Clark, Madison, Meagher, Park, Powell, Sweet Grass.

Neominois Scudder, 1875

163   *ridingsii ridingsii* (W. H. Edwards)—Beaverhead, Blaine, Broadwater, Carbon, Chouteau, Dawson, Fergus, Gallatin, Jefferson, Lewis & Clark, Madison, Park, Sweet Grass.

Cercyonis Scudder, 1875

164   *pegala ino* (Hall)—Beaverhead, Big Horn, Blaine, Carbon, Cascade, Chouteau, Custer, Dawson, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Hill, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Mineral, Missoula, Musselshell, Park, Phillips, Powder River, Powell, Prairie, Ravalli, Sanders, Stillwater, Sweet Grass, Yellowstone.

165   *meadii meadii* (W. H. Edwards)—Carbon, Custer, Dawson, Musselshell, Yellowstone.

166   *sthenele paulus* (W. H. Edwards)—Beaverhead, Carbon, Mineral. This species is included on the basis of records from James A. Scott and C. J. Durden. I have not seen the specimens.

167   *oetus charon* (W. H. Edwards)—Beaverhead, Blaine, Broadwater, Carbon, Cascade, Chouteau, Custer, Dawson, Flathead, Gallatin, Glacier, Granite, Jefferson, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Mineral, Missoula, Park, Powder River, Powell, Prairie, Ravalli, Sanders, Silver Bow, Stillwater, Sweet Grass, Valley. Included here are records which reported *phocus* (W. H. Edwards).

Oeneis Hübner, 1816

168   *uhleri varuna* (W. H. Edwards)—Blaine, Broadwater, Carbon, Cascade, Chouteau, Custer, Dawson, Fallon, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Granite, Jefferson, Lewis & Clark, Meagher, Missoula, Musselshell, Powell, Sweet Grass, Wibaux, Yellowstone.

169   *chryxus chryxus* (Doubleday)—Beaverhead, Carbon, Cascade, Deer Lodge, Fergus, Flathead, Gallatin, Glacier, Granite, Judith Basin, Lake, Lewis & Clark, Lincoln, Madison, Meagher, Missoula, Park, Powell, Ravalli, Sanders, Silver Bow, Sweet Grass.

170   *alberta alberta* Elwes—Fergus, Glacier, Golden Valley, Hill, Judith Basin.

171   *taygete edwardsi* dos Passos—Carbon, Stillwater.

172   *jutta reducta* McDunnough—Beaverhead, Cascade, Jefferson, Judith Basin, Lewis & Clark, Meagher, Missoula, Powell. The more northern Montana representatives of *jutta* are placed as *reducta* for the present, but specimens require further study.

173   *melissa beanii* Elwes—Carbon, Glacier, Stillwater.

Erebia Dalman, 1816

174   *magdalena magdalena* Strecker—Carbon.

175   *theano ethela* W. H. Edwards—Carbon, Park, Stillwater.

176a *epipsodea epipsodea* Butler—Beaverhead, Broadwater, Carbon, Deer Lodge, Flathead, Gallatin, Glacier, Granite, Jefferson, Lake, Lewis & Clark, Lincoln, Madison, Mineral, Missoula, Park, Powell, Ravalli, Sanders, Silver Bow, Stillwater, Sweet Grass.

176b *epipsodea freemani* Ehrlich—Cascade, Chouteau, Fergus, Judith Basin, Meagher.

177   *callias callias* W. H. Edwards—Carbon.

ACKNOWLEDGMENTS

LITERATURE CITED

BROWN, F. M. 1972. *Pseudophilotes* Beuret, 1958. J. Lepid. Soc. 26: 111.
———— & W. D. FIELD. 1970. *Papilio hyllus* Cramer, 1776, vs. *Polyommatus thoe* Guérin-Méneville, 1831, and the "50-year rule" (Lepidoptera: Lycaenidae). J. N. Y. Entomol. Soc. 78: 175–184.
CLENCH, H. K. 1944. Two new subspecies of *Everes comyntas* Godart (Lepidoptera, Lycaenidae). J. N.Y. Entomol. Soc. 52: 59–61.
COOLIDGE, K. R. 1906. Review: "The Butterflies of Montana," M. J. Elrod. Entomol. News 17: 263.
————. 1909. *Melitaea gillettei* Barnes. Entomol. News 20: 137.
DALY, H. V. 1964. Rare butterflies from Montana. Pan-Pacific Entomol. 40: 64.
EDWARDS, W. H. 1872. List of species of butterflies collected by Campbell Carrington and William B. Logan, of the Expedition, in 1871. pp. 466–467 *in*: F. V. Hayden, Preliminary report of the United States Geological Survey of Montana and portions of adjacent territories, being a fifth annual report of progress. Govt. Printing Office, Wash., D.C., 538 p.
————. 1878. On the Lepidoptera collected by Dr. Elliot Coues, U.S.A., in Montana, during 1874. Bull. U.S. Geol. & Geog. Sur. Terr. 4: 513–517.
————. 1882a. Descriptions of two new species of N. American butterflies. Can. Entomol. 14: 2–6.
————. 1882b. List of butterflies taken by H. K. Morrison in Dacotah and Montana, 1881. Can. Entomol. 14: 6.
————. 1883. Notes on a small collection of butterflies, made in Judith Mtns., Montana in 1883, by Wm. M. Courtis, M.E. Papilio 3: 157–164.
————. 1886. Descriptions of new species of butterflies found in the United States. Can. Entomol. 18: 61–65.
————. 1890. Notes on *Erebia epipsodea*, Butler. Can. Entomol. 22: 48–52.

————. 1894. Description of the preparatory stages of *Phyciodes carlotta*, Reakirt. Can. Entomol. 26: 3–8.

ELROD, M. J. 1906. The Butterflies of Montana, Univ. of Montana Bull. 30: 1–174.

———— & J. H. MASTERS. 1970. The butterflies of Montana, Mid-Cont. Lepid. Ser. 1(17): 1–14.

FERRIS, C. D. 1973. A revision of the *Colias alexandra* complex (Pieridae) aided by ultraviolet reflectance photography with designation of a new subspecies. J. Lepid. Soc. 27: 57–73.

————. 1976a. A proposed revision of non-arctic *Parnassius phoebus* Fabricius in North America (Papilionidae). J. Res. Lepid. 15: 1–22.

————. 1976b. A note on the subspecies of *Parnassius clodius* Menetries found in the Rocky Mountains of the United States (Papilionidae). J. Res. Lepid. 15: 65–74.

————. 1977. Taxonomic revision of the species *dorcas* Kirby and *helloides* Boisduval in the genus *Epidemia* Scudder (Lycaenidae: Lycaeninae). Bull. Allyn Mus. 45: 1–42.

FIELD, W. D. 1936a. Three new butterfly races (Lepid.: Nymphalidae, Lycaenidae). Entomol. News 47: 121–124.

————. 1936b. New North American Lepidoptera. J. Entomol. & Zool. (Pomona College) 28: 17–26.

————. 1938. A new race of *Lycaena mariposa* (Reakirt) (Lepid. Lycaenidae). Pan-Pacific Entomol. 14: 142–143.

FISHER, M. S. 1977. The taxonomy and identity of *Papilio nitra* W. H. Edwards in Colorado (Papilionidae). Bull. Allyn Mus. 47: 1–8.

HIGGINS, L. G. 1978. A revision of the genus *Euphydryas* Scudder (Lepidoptera: Nymphalidae). Entomol. Gaz. 29: 109–115.

HOWE, W. H. 1975. The Butterflies of North America. Doubleday, Garden City, 633 p.

JOHNSON, K. 1976. Three new nearctic species of *Callophrys* (*Mitoura*), with a diagnostis of all nearctic consubgeners (Lepidoptera: Lycaenidae). Bull. Allyn Mus. 38: 1–30.

KOHLER, S. 1977. Revision of North American *Boloria selene* (Nymphalidae) with description of a new subspecies. J. Lepid. Soc. 31: 243–268.

MATTONI, R. H. T. 1977. The Scolitantidini I: Two new genera and a generic rearrangement (Lycaenidae). J. Res. Lepid. 16: 223–242.

McDUNNOUGH, J. H. 1928. A new *Euphydryas* (Lepidoptera). Can. Entomol. 60: 248–249.

————. 1929. Notes on some diurnal Lepidoptera from Yellowstone Park and the adjacent regions of Montana. Can. Entomol. 61: 105–107.

MILLER, L. D. & F. M. BROWN. 1979. Studies in the Lycaeninae (Lycaenidae) 4. The higher classification of the American coppers. Bull. Allyn Mus. 51: 1–30.

SCUDDER, S. H. 1875. Report on the butterflies collected by Mr. J. A. Allen on the Yellowstone expedition of 1873. Proc. Boston Soc. Nat. Hist. 17: 86–91.

SHAPIRO, A. M. 1976. The biological status of nearctic taxa in the *Pieris protodice-occidentalis* group (Pieridae). J. Lepid. Soc. 30: 289–300.

SHEPARD, J. H. 1964. The genus *Lycaeides* in the Pacific Northwest. J. Res. Lepid. 3: 25–36.

SHIELDS, O. 1975. Studies on North American *Philotes* (Lycaenidae) IV. Taxonomic and biological notes, and new subspecies. Bull. Allyn Mus. 28: 1–36.

SKINNER, H. 1893. Notes on *Argynnis cybele* and *leto*. Entomol. News 4: 318–319.

————. 1921. A new species of *Melitaea* from Montana (Lepid., Rhop.). Entomol. News 32: 89.

STALLINGS, D. B. & J. R. TURNER. 1947. New American butterflies. Can. Entomol. 78: 134–137.

WILEY, C. A. 1894. Butterflies at Miles City, Montana. Entomol. News 5: 36–38.

WRIGHT, W. S. 1922. A new lycaenid (Lepidoptera). Bull. So. Calif. Acad. Sci. 21: 19–20.

A NEW *PLEBEJUS* (*ICARICIA*) *SHASTA* (EDWARDS) FROM SOUTHERN NEVADA (LYCAENIDAE)

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ABSTRACT. The distinctive population of *Plebejus* (*Icaricia*) *shasta* (Edwards), known only from the Spring Range (Clark Co.) Nevada, is described as the new subspecies, *P. s. charlestonensis*. No intermediate populations are known. Its abundance varies widely from year to year. The distinctness of this and other endemic taxa further confirms the isolation of the fauna of the Spring Range.

In his recent revision of the *Plebejus* (*Icaricia*) *shasta* (Edwards) complex, Ferris (1976) failed to recognize the distinctive population occurring at the higher elevations of the Spring Range in Clark County, Nevada. The first mention of this population was by Garth (1928) who recognized it as distinct from nominate *shasta* of California; its difference from other *shasta* populations was further reiterated by Emmel and Shields (in press). The Spring Range specimen illustrated in Howe (1975) was designated *shasta shasta* form "comstocki." Ferris (1976) included Spring Range material with the wide-ranging *P. shasta minnehaha* (Scudder). Ferris (1976) saw no reason to describe local isolated colonies as new taxa. However, in light of the distinctiveness of Spring Range *shasta* and of the occurrence of at least three well defined races of other butterflies endemic to the mountains of southern Nevada, it seems appropriate to name this population of *P. shasta*.

Plebejus shasta charlestonensis, new subspecies

(Fig. 1)

Male (based on holotype and 6 topoparatypes) **dorsal surface.** Primaries bright violet-blue (near Mauve, all capitalized colors herein after Smithe, 1975); discal cell spot black and prominent; wing border black, narrow and sharply defined with few black scales extending basad except along the veins; fringe entirely white. Secondaries of same ground color as primaries; marginal spots large and well defined occurring in cells Rs through Cu_2 with those in Rs and Cu_2 occasionally blurred and that in Cu_1 the largest. Distad to the marginal spots, a well defined pale gray (nearly white) line interrupted by black-scaled veins; the black scaling of the veins extending proximally to somewhat basad of the marginal spots; discal cell spot narrow and not particularly prominent. Distal to the pale marginal line, a black terminal band adjacent to a pure white fringe; fringe on the inner (anal) margin pale gray-brown somewhat paler than the gray-brown scales along the inner margin of this wing. **Ventral surface.** Primaries clear pale gray (Pale Neutral Gray) fading to brownish gray; a large elongate black spot at the distal end of discal cell and another smaller spot in the middle part of this cell in all seven specimens. Post-median spot row composed of large black spots except in
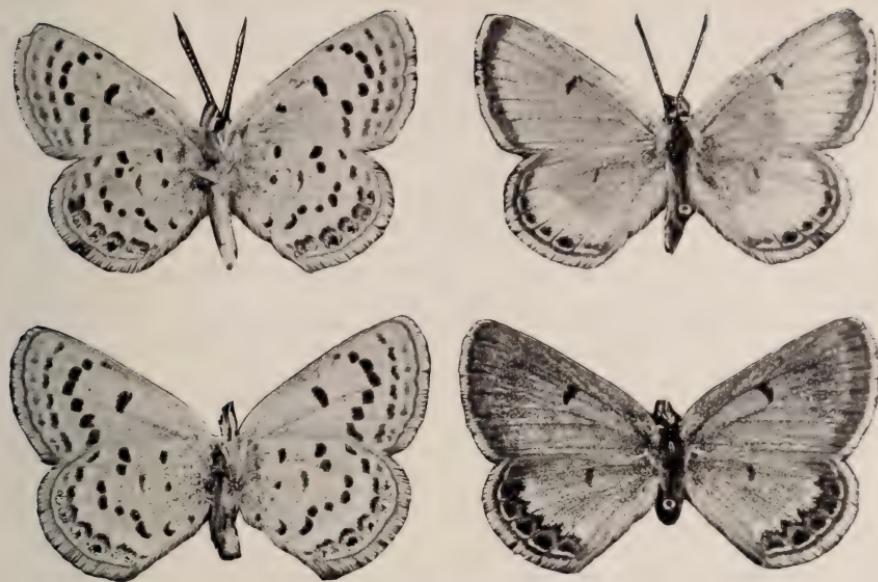
FIG. 1. *Plebejus shasta charlestonensis* n. ssp. Left: ventral surface of holotype ♂ (upper) and allotype ♀ (lower). Right: dorsal surface of holotype ♂ (upper) and allotype ♀ (lower). Photos by R. Aseltine.

Cu_2 where the spot is dark gray in most specimens; all spots heretofore mentioned narrowly and indistinctly outlined with pale gray. The submarginal spot row brownish-gray; the marginal row a similar but paler color. Terminal line brownish-gray bordering a white fringe. Secondaries slightly paler than primaries with all spots in the post-median row and basal area black and indistinctly outlined with pale gray. In some specimens the posterior spots (beyond M_1) with a slight brownish-gray cast as the spot in the end of the discal cell. Marginal metallic Apple Green spots in cells M_1 to Cu_2 centered with black and capped with clear orange (near Chrome Orange) lunules which are in turn capped with black; basal to this a very pale gray area grading into the gray-brown ground color of the rest of the wing; a narrow, pale gray line separating the metallic spots from a brownish-gray terminal line adjacent to a white fringe. The marginal-submarginal pattern weakly represented in cell Rs of some specimens and usually represented only by black submarginal spots in this and cell Sc + R_1.

Female (based on allotype and six topoparatypes) **dorsal surface.** Primaries dark brownish-black with an extensive violet-blue overlay of about the same color as the male; this overlay extending from the wing base to at least the end of the discal cell and in most specimens to at least 50% further towards the outer margin along the inner margin of the wing; the costal margin (except basally) and the apical area without the violet-blue overlay. The discal cell spot prominent and averaging larger than in the male. Secondaries of the same dark brownish-black ground color as the primaries with the entire basal portion posterior to M_1 overlaid with violet-blue, this extending distally to the marginal-submarginal band. The marginal black spots large and black, often pointed basally and largest in Cu_1; these capped basally with broad orange to orange-brown (most specimens near Chrome Orange) lunules, interrupted from forming a complete band by relatively indistinct black-scaled veins; the orange lunules bordered

basally by a distinct black band; adjacent to the latter, in some specimens, an area devoid of the blackish ground color which makes the violet overlay appear as a very pale violet color; distal to the black marginal spots, a narrow, but distinct, pale gray line; the white fringe bordered inwardly by a black band. The marginal pattern indistinctly represented in cell Rs in some specimens. The inner marginal area and its fringe similar to the male. **Ventral surface.** Quite similar to the male but the post-median spots tending larger on both the primaries and secondaries. Three of the seven specimens with a mid-discal cell spot on the primaries.

Types[2]. Holotype ♂: Lee's (=Lee) Canyon, (Spring Range), Clark Co. (unty), Nev. (ada), 8,500′, 21 July 1963. Allotype ♀: Lee's (=Lee) Canyon, (Spring Range), Clark Co. (unty), Nev. (ada), 8,250′, 21 July 1963. This specimen lacks the right antenna and most of the left. Topoparatypes: 6♂, Lee's (=Lee) Canyon, (Spring Range), Clark Co. (unty), Nev. (ada), 8,250′, 21 July 1963; 4♀, Lee's (=Lee) Canyon, (Spring Range), Clark Co. (unty), Nev. (ada), 8,250′, 21 July 1963; 1♀, same data except 8,550′; 1♀, same data except 8,800′. Entire type series collected by George T., Anna T. and Edward J. Austin.

Deposition of type material. The holotype and allotype will be deposited in the Los Angeles County Museum, Los Angeles, California; a pair of topoparatypes will be deposited in the Nevada State Museum, Carson City, Nevada; the remaining topoparatypes will be retained by the author.

Type locality. NEVADA: Clark Co.; Spring Range, Lee Canyon, 8,250–8,800′. This is the open area between Lee Canyon Guard Station and the ski tow as shown on USGS Charleston Peak, Nevada, quadrangle, 15 minute series (R 56E, T 18S, S 10 and S 15) and virtually surrounded by a forest of Ponderosa and Bristlecone pines (*Pinus ponderosa* Dougl. and *P. aristata* Engelm.) and White Fir (*Abies concolor* (Gord.) Parry).

Additional specimens examined. (all NEVADA: Clark Co., Spring Range) Kyle Canyon Road above chain, ca. 8,500′, 27 July 1965 (1♀); Kyle Canyon, 9,000′, 25 July 1965 (1♂, both Austin collection); Lee Canyon (near ski area), 5 July 1976 (1♂, D. Mullins collection). **Other known specimens.** (all NEVADA: Clark Co.; Spring Range) Willow Creek, 6,000–8,000′, 15 July 1928 (15♂ 19♀, Gunder collection in American Museum of Natural History, fide J. F. Emmel); Lee Canyon Ski Run, 8,600′, 12 and 17 August 1963 (8 specimens, J. F. Leser collection); Cathedral Rock (Kyle Canyon) 8,500′, 10 July 1972 (1 specimen, D. E. Allen collection); road between Kyle Canyon Camp and Deer Creek Camp (=Deer Creek Road), ca. 7,000′, 1 July 1950 (2♀, from field notes of F. W. Preston where listed as *Plebius* (sic) *acmon*, one of these illustrated in Howe, 1975). The specimens in the Gunder collection must be part of the series of "several hundred" collected by Morand as mentioned by Garth (1928). The fate of the remaining specimens of this series is unknown to the author.

Geographic range, phenology and abundance. To date, *P. shasta charlestonensis* is known only from the Spring Range between 6,000 and 9,000′ in the Kyle Canyon–Lee Canyon areas and in the northern part of the range near Willow Creek. The known flight period of the single brood extends from 5 July to 17 August, probably peaking in late July. It apparently varies greatly in abundance as numerous specimens were taken in 1928 and 1963, 2 specimens in 1965 and one in 1976. No other specimens are known although areas close to known collection sites of *P. shasta* are visited regularly by collectors seeking the other Spring Range endemics. In 1977, I collected extensively in Kyle Canyon and at Willow Creek throughout the summer and was at the type locality in Lee Canyon on 7 and 29 July but no *shasta* were seen.

Etymology. This subspecies is named after the highest peak in the Spring Range and a popular name for the main mass of the Spring Range.

Discussion. The new subspecies is the most distinctive of the races of *P. shasta*.

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[2] Data on types are as indicated on specimen labels, parenthetical data correct errors or clarify label data.

Its closest relationships appear to be with the Great Basin populations allied to *P. s. minnehaha*. The dorsal ground coloration of males is as bright or brighter than *minnehaha* with more violet and less blue (other populations, including nominate *shasta*, tend towards Campanula). Its narrow borders are like those of *minnehaha* and contrast with the broad borders of nominate *shasta*. Beneath, the pattern is clear and bold with less tendency for the post-median spot row to fade into the ground color. This in itself distinguishes the taxon. The orange submarginal lunules are a clear, Chrome Orange and not dull (usually near Cinnamon Rufous) as in the other races. The females are even more strongly different from those of other *shasta* populations. The violet-blue overscaling is extensive, covering about 75% of the dorsal wing surfaces and of the same color as in males. The marginal pattern of the dorsal hind wing is very prominent with large marginal black spots capped broadly with orange lunules which are set off from the violet wing coloration by a broad dark band. The orange band is broad and clearly defined in all female *charlestonensis* examined; it is often narrow and/or indistinct and overscaled with black in females from other populations. The ventral surface pattern is clear and bold as in males. The post-median spot row of the ventral secondaries tends to approach closer to the marginal band especially towards the anal angle. In many respects the females of this population of *P. shasta* superficially resemble *Plebejus acmon* (Westwood and Hewitson). The painting of the Spring Range *P. shasta* in Howe (1975, plate 59, Fig. 16) is a fairly good representation of the female of this new subspecies.

The justification for naming this population aside from its definite pattern differences from other *shasta* populations lies in the isolation of the Spring Range (and the nearby Sheep Range) from other mountain masses of similar elevation by some 75 miles of low, arid desert. This isolation has resulted in the differentiation of three named taxa of other butterflies: *Limenitis weidemeyerii nevadae* (Barnes & Benjamin), *Euphydryas anicia morandi* Gunder and *Speyeria zerene carolae* (dos Passos & Grey). Endemism is known for other taxa including plants (Clokey, 1951), mammals (Hall, 1946) and, to some degree, birds (Johnson, 1965).

Ferris (1976) included all Nevada *shasta* in *minnehaha* but he did not have material from the Sierra Nevada of extreme western Nevada. I have examined over 100 Nevada specimens (outside Clark County) in the Nevada State Museum and my personal collection. Specimens from Washoe Co. (Mt. Rose, Hobart Reservoir) and Ormsby Co. (Snow Valley) are clearly within the concept of nominate *shasta*. Those from Elko (Angel Lake) and White Pine (Mt. Wheeler, Stella Lake, Bald Mt.) counties are best referred to unnamed populations allied to *minnehaha* (see Emmel and Shields, in press). Material from Lander (Mahogany Canyon), Mineral (Corey Peak), Esmeralda (Trail Canyon) and possibly Douglas (Mt. Siegel) and Pershing (Star Peak) counties appear intermediate between these unnamed segregates and nominate *shasta*. None of these populations shows any intermediacy towards *charlestonensis*.

LITERATURE CITED

CLOKEY, I. W. 1951. Flora of the Charleston Mountains, Clark County, Nevada. Univ. Calif. Publ. Botany, No. 24.

EMMEL, J. F. & O. SHIELDS. The biology of *Plebejus (Icaricia) shasta* in the western United States (Lycaenidae). J. Res. Lepid., in press.

FERRIS, C. D. 1976. Revisionary notes on *Plebejus (Icaricia) shasta* (Edwards). Bull. Allyn Museum, No. 36.

GARTH, J. S. 1928. Report of the Lorquin Entomological Society of Los Angeles. Proc. So. Calif. Acad. Sci. 27: 93–94.

HALL, E. R. 1946. Mammals of Nevada. Univ. Calif. Press, Berkeley.

HOWE, W. H. 1975. The butterflies of North America. Doubleday, Garden City, N.Y.

JOHNSON, N. K. 1965. The breeding avifaunas of the Sheep and Spring ranges in southern Nevada. Condor 67: 93–124.

SMITHE, F. B. 1975. Naturalist's color guide. Am. Mus. Nat. Hist., New York.

THE IDENTITY OF THE PLANT REFERRED TO AS *ANDROMEDA* BY W. T. M. FORBES

The name Andromeda has been used ambiguously in the lepidopteran literature. A striking example is in its mention as a larval host for *Datana major* Grote and Robinson and *Datana ranaeceps* (Guérin) by Forbes (1948, Lepidoptera of New York . . . II: Cornell U. Agric. Expt. Sta. Mem. 274, p. 215). The ranges of both of these species lie almost entirely to the south and east of the only species of the genus *Andromeda* covered by Fernald (1950, Gray's Manual of Botany, 8th ed. Amer. Book Co., N.Y., p. 1123). Furthermore, Robinson and Fernald (1908, Gray's New Manual of Botany, 7th ed., Amer. Book Co., p. 635) list *Andromeda* as an old generic name for three species of *Lyonia*. They also include *Pieris floribunda* (Push) B. & H. in *Andromeda*. In an earlier work, Forbes (1923, Lepidoptera of New York . . . I: Cornell U. Agric. Expt. Sta. Mem. 68, p. 700) makes the following citation in the food index "Andromeda (Andromeda, Lyonia): villela 312." The moth (*Holcocera villela* Busck) is listed in the text as feeding on *Andromeda ligustrina*, a plant placed in *Lyonia* by Fernald (1950) and Robinson and Fernald (1908).

I have repeatedly found eggs and larvae of both of the above *Datana* on *Lyonia mariana* (L.) D. Don. in the New Jersey Pine Barrens. *D. major* also utilizes *Leucothoe racemosa* (L.) Gray about equally often. Older larvae of both occasionally wander to highbush blueberries (*Vaccinium* 2 or 3 spp.). No species of *Pieris* or *Andromeda* is native to that region.

Thus, lepidopterists should consider host records of Andromeda (or *Andromeda*) cautiously unless the species is stated. It is virtually certain that such records for *Datana* and probably *Catocala andromedae* (Guenée) (Forbes, 1954, Lepidoptera of New York . . . III, Cornell U. Agric. Expt. Mem. 329, p. 333) actually refer to some species of *Lyonia*.

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NIGERIAN GRACILLARIIDAE

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ABSTRACT. Ten gracillariids new to Nigeria are recorded, of which five are newly described. The previously undescribed species are *Epicephala suttoni* n. sp., *Acrocercops pectinivalva* n. sp., *A. fuscapica* n. sp., *Spulerina quadrifasciata* n. sp. and *Phyllonorycter caudasimplex* n. sp. A list of the 16 species now known from West Africa is included. Three species are given as new combinations; they are *Acrocercops bifasciata* (Walsingham, 1891) n. comb., *A. leucostega* (Meyrick, 1932) n. comb. and *Phyllonorycter loxozana* (Meyrick, 1936) n. comb.

A small collection of gracillariid moths from Nigeria has yielded the following new records and new species:

Ectropina sclerochitoni Vári, 1961. 2♀♀, Ibadan, NIGERIA. 15.I.1972, K. Bland [Genitalia, BM(NH) slide 21281. The imago from which this slide was made was later accidentally destroyed; the other ♀ is without an abdomen!] This species has not previously been recorded from Nigeria.

Epicephala suttoni, n. sp.

Description. Alar expanse 8 mm, ♀ (see Fig. 1a). Head with scales appressed on crown, projecting in front; head and face white, mixed with very pale fuscous on crown. Antennae pale ochreous-brown. Labial and maxillary palps white tinged with fuscous. Tegulae ochreous-brown. Thorax whitish. Anterior surface of all legs fuscous; posterior aspect transversely barred fuscous and white.

Forewings pale ochreous-brown tending to chestnut-brown in apical area; three very oblique white lines running outwards from costa at ¼, ½ and ⅔ reaching only ½ across the wing; a curved shiny silver-grey transverse fascia before apical area; dorsum thinly edged white with a short oblique spur just past ⅓; an indistinct curved, oblique, white, double line from just past ½ dorsum to near middle of silver-grey fascia; apical spot chocolate brown, apex edged with same colour and lined inwardly with white; apical cilia white but with dark brown tips above apex. (Hindwings missing.)

Female genitalia (see Fig. 2a). Papillae anales minute, hairless and bluntly pointed: ostium bursae large with a large oblong lamella antevaginalis; posterior margin of latter incurved with a central square indentation; antrum sclerotized, slightly curved and widening posteriorly; ductus bursae and bursa copulatrix membranous; many small pegs at junction of antrum and ductus bursae [Genitalia, BM(NH) slide 21275].

Type specimens. Holotype ♀ only. At light at University College, Ibadan, NIGERIA. 13.I.58, H. J. Sutton. Type in British Museum (Natural History), London.

Remarks. Very similar in wing pattern and genitalia to *E. homostola* Vári, 1961 but readily separated from it by the shape of the lamella antevaginalis.

Aristaea onychota (Meyrick, 1908). 1♂, Ibadan, NIGERIA. 15.I.1972, K. Bland [Genitalia, BM(NH) slide 21282]. This species has not previously been recorded from Nigeria.

Stomphastis conflua (Meyrick, 1914). 11♂♂ & ♀♀, University College, Ibadan, NIGERIA. 3.V.1962, G. H. Caswell [Genitalia slides B181, B189, BM(NH) slide 21286]. 2♂♂, Ile-Ife, NIGERIA. 25.VII.1970 & 15.VIII.1970, J. T. Medler [Gen. BM(NH) slides 21284, 21285]; 1♂, Ibadan, NIGERIA. 8.XII.1971, K. Bland [Gen. slide B236].

The genitalia of the male differ slightly from Vári's figure and description of the type (Vári, 1961) in that the tip of the valve is more falcate and the cornutus on the aedoeagus is forked (see Fig. 3a). In the female the distance of the ostium from the anterior margin
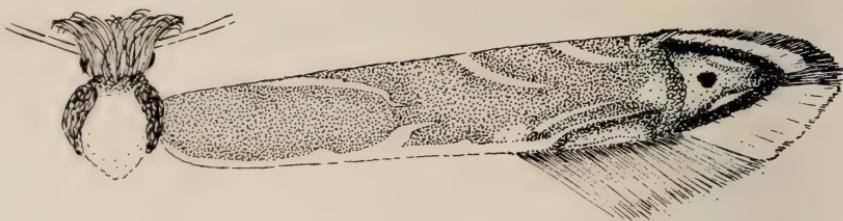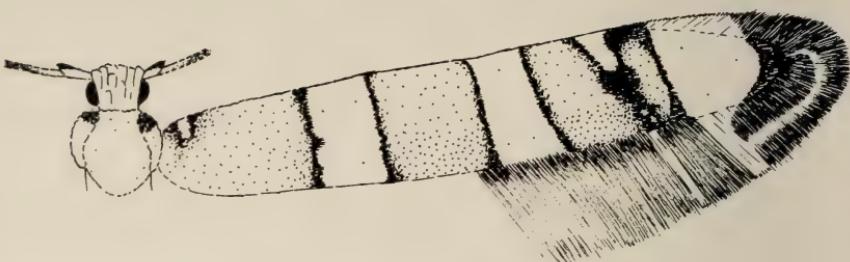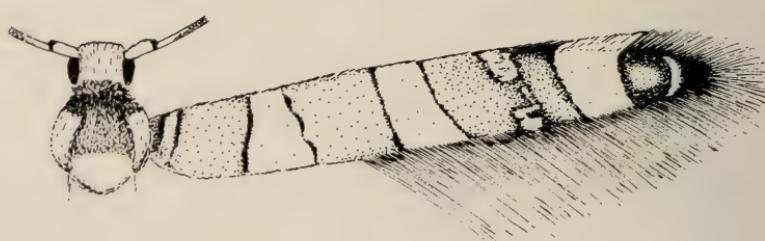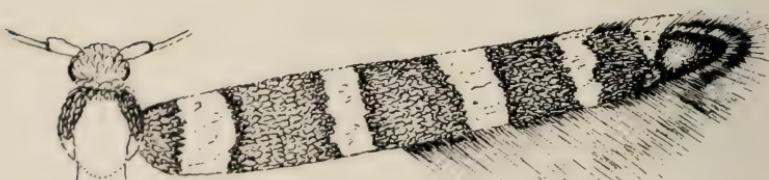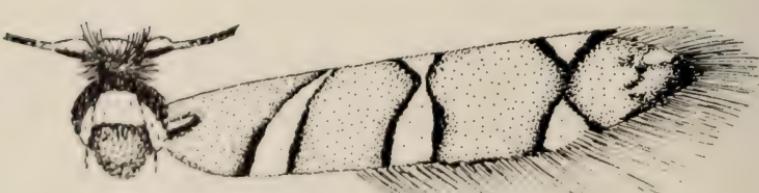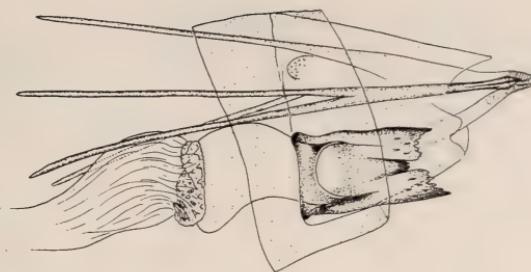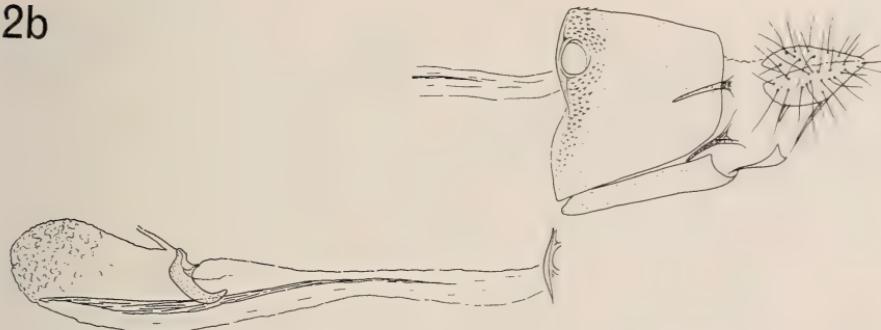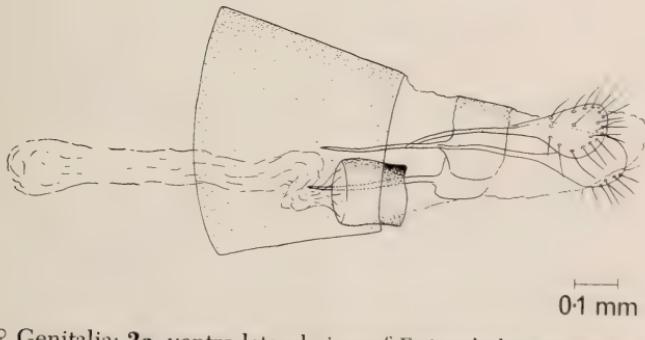
FIG. 2. ♀ Genitalia: **2a,** ventro-lateral view of *Epicephala suttoni* n. sp.; **2b,** dorso-lateral view of *Stomphastis conflua* (Meyr.); **2c,** ventro-lateral view of *Phyllonorycter caudasimplex* n. sp.

←

FIG. 1. Head, thorax and right forewing of the new species described in the text. **1a,** *Epicephala suttoni*; **1b,** *Acrocercops pectinivalva*; **1c,** *A. fuscapica*; **1d,** *Spulerina quadrifasciata*; **1e,** *Phyllonorycter caudasimplex*. (Not to scale).
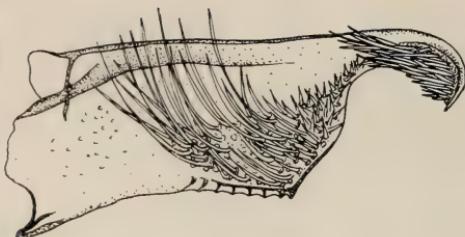
FIG. 3. ♂ Genitalia: **3a,** valve and aedoeagus of *Stomphastis conflua* (Meyr.); **3b,** valve and aedoeagus of *Lamprolectica apicistrigata* (Wals.); **3c,** dorso-lateral view of *Acrocercops bifasciata* (Wals.).

of the segment is shorter and the hooked signum apparently larger in the present specimens (see Fig. 2b). Although not previously recorded from West Africa, these slight differences are probably only geographical variations. One of the two foodplants recorded by Vári (1961), namely *Ricinus communis* Linn. (Euphorbiaceae) is recorded from Nigeria (Thiselton-Dyer, 1913).

Lamprolectica apicistrigata (Walsingham, 1891) 1♂, 1♀, Ibadan, NIGERIA. 28.XII.1971, K. Bland; 1♂, Ibadan. 21.I.1972, K. Bland [Genitalia, BM(NH) slide 21280].

In the ♂ genitalia, the ventral projection of the valve (see Fig. 3b) is not present in Vári's figure or description but is present in Walsingham's type [BM(NH) slide 4036 in British Museum of Natural History, London]; however due to the way the genitalia are mounted it is difficult to discern. This species has previously only been recorded from Gambia and South Africa.

Acrocercops pectinivalva, n. sp.

Description. Alar expanse 7 mm, ♂ (see Fig. 1b). Head white, with appressed scales. Labial palps dark fuscous; apical segment white. Maxillary palps dark fuscous mixed whitish. Antennae pale ochreous-brown distally; whitish basally. Legs white ringed with blackish. **Forewings** brown suffused towards costa with chestnut-brown except basally; three broad white fasciae, edged with dark brown, at ⅓, ⅔ and before apex; first two parallel-sided and slightly outwardly oblique from costa; third occupying most of apical area, extending into the apical cilia and broadest on the costa; extreme apex dark brown; a small white oblique mark on costa nearer to apical than median fascia, continued across wing as a dark brown line; apical cilia dark brown, except opposite fascia, with a white subterminal band from apex to dorsal part of apical fascia. Hindwings dark fuscous, cilia paler.

Male genitalia (see Fig. 4a). Tegumen membranous, with fine hairs on underside; valvae broad at base, then up-curved and parallel-sided; cucullus bluntly pointed; a single comb of teeth extending along posterior half of ventral margin; aedoeagus long, rather stout and produced into a sclerotized point; one pair of long coremata [Genitalia, BM(NH) slide 21276].

Type specimens. Holotype ♂ only. At light on University of Ibadan campus, Ibadan, NIGERIA. 29.I.1972, K. Bland. Type in the British Museum (Natural History), London.

Remarks. Most closely related by genitalia to *A. odontosema* Vári, 1961 to which it shows slight superficial resemblance; the shape of the valve and length of the comb separate it from all other species of the genus.

Acrocercops bifasciata (Walsingham, 1891) n. comb.

1♂, Ile-Ife, NIGERIA. 17.IX.1971, J. T. Medler [Genitalia, BM(NH) slide 21283]; 2♀♀, Ibadan, NIGERIA. 26 & 28.XII.1971, K. Bland [Gen. slide B114].

Originally described in the genus *Gracillaria* it is now transferred to *Acrocercops*. The ♂ genitalia (see Fig. 3c) agree with those of the holotype from Gambia in the British Museum of Natural History, London [BM(NH) slide 4037]. This species has not previously been recorded from Nigeria.

Acrocercops fuscapica, n. sp.

Description. Alar expanse 6 mm, ♂ (see Fig. 1c). Head white, with appressed scales; crown and lower face shining pale ochreous-brown. Labial palps white tinged darker in parts; tips blackish. Maxillary palps white; dark fuscous apically. Antennae shining pale ochreous-brown, paler basally; basal segment of antenna and scape white; scape dark fuscous distally. Collar white. Tegulae and thorax shining pale ochreous-brown; white caudally. Legs white, banded with dark fuscous. **Forewings** pale orange-brown; three broad white almost parallel-sided fasciae, thinly edged with dark brown,

4a

4b

0·1 mm

4c

0·1　mm
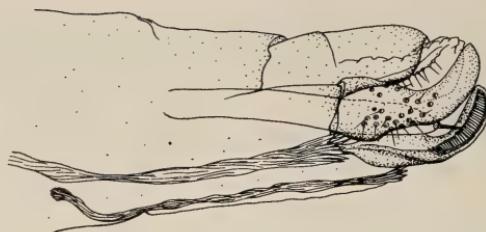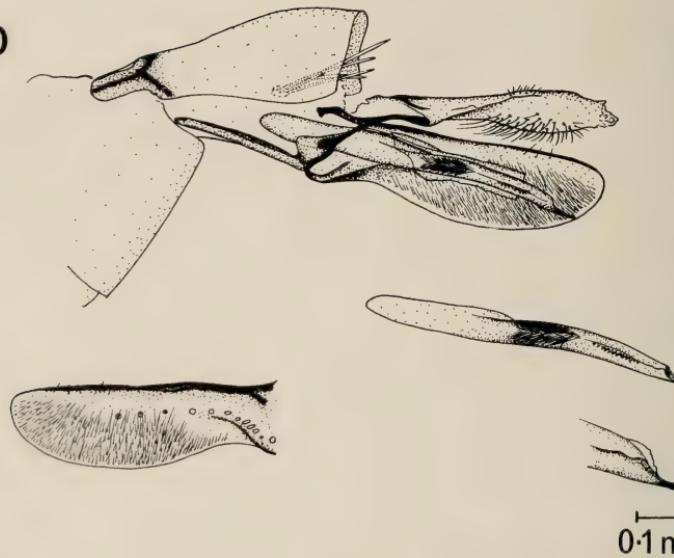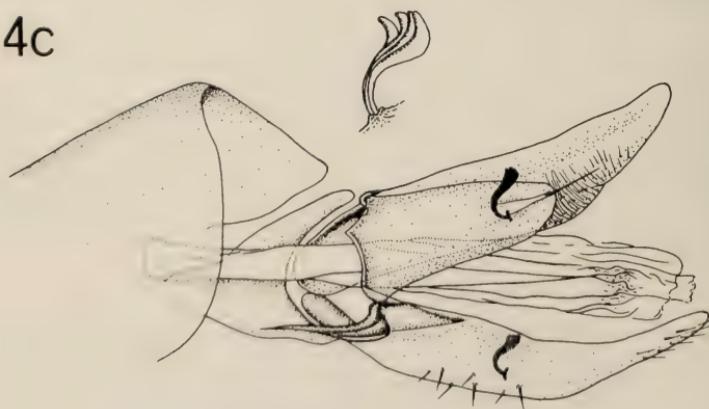
at just over ¼, ½ and at ⅘; an indistinct narrow whitish fascia between the last two and another at the base; apical area and cilia dark brown; apical spot orange-brown edged outwardly with some white scales. Hindwings grey; cilia darker grey.

Male genitalia (see Fig. 4b). Tegumen almost membranous, underside with fine hairs; valva simple, costa straight, apex rounded, ventral margin curved; disc covered with fine hairs; vinculum narrow; saccus rod-shaped and ½ length of valva; aedoeagus long, slender, almost straight; tip extended into a pair of sclerotized prong-like projections; vesica with rough sclerotized area; 8th tergite weakly sclerotized with a sclerotized median prong anteriorly [Genitalia, BM(NH) slide 21277].

Type specimens. Holotype ♂ only. Ile-Ife, NIGERIA. 11.I.1972, J. T. Medler. Type in British Museum (Natural History), London.

Remarks. Superficially very similar to *A. gossypii* Vári, 1961 but the forewings are more orange and the apical fascia is larger. It is readily separated from *gossypii* by the structure of the ♂ genitalia, in which the valves are more rounded and the saccus more elongate.

Spulerina quadrifasciata, n. sp.

Description. Alar expanse 6 mm, ♂ (see Fig. 1d). Head, with appressed scales, ochreous-white; face white becoming more ochreous ventrally. Antennae dark fuscous above, except basally; underside whitish; the broad scape ochreous-white above; underside dark fuscous. Labial palps white with apex of segments 2 and 3 suffused fuscous. Maxillary palps dark fuscous but with apical segment paler. Legs white with broad fuscous rings. **Forewings** purplish-fuscous, mixed ochreous-fuscous; transverse, parallel-sided white fasciae with dark edges, near base, at just over ¼ and ½; another less regular fascia at ¾; an indistinct white triangular patch on costa before apex and another opposite at tornus; apical area dark fuscous; apical cilia fuscous mixed with white, becoming ochreous after tornus. Hindwings and cilia pale fuscous, tinged ochreous.

Male genitalia (see Fig. 4c). Uncus rounded at apex and with a single median spine; valva with ventral margin parallel to costal margin to ⅔ then obtusely angulated; on inner surface at ½, a small comb with 4 lamellae and a very narrow base; aedoeagus rather long and stout, membranous with no cornuti [Genitalia, BM(NH) slide 21278].

Type specimens. Holotype ♂ only. At light at University of Ibadan campus, Ibadan, NIGERIA. 12.I.1972, K. Bland. Type in the British Museum (Natural History), London.

Remarks. Very similar in wing coloration to *S. hexalocha* (Meyrick, 1912) but not in genitalia structure (Vári, *in litt.*). The genitalia show a closer affinity to *S. simploniella* (Fischer von Röslerstamm, 1844) from which they differ primarily in the valves being less produced apically and the comb on the valve having fewer lamellae.

Phyllonorycter caudasimplex, n. sp.

Description. Alar expanse 7 mm, ♀ (see Fig. 1e). Face and palpi shining white; crown of head rough-haired and chestnut-brown. Antennae ringed fuscous and pale ochreous-brown; basal segment white but chestnut-brown dorsally. Thorax shining white anteriorly and pale fuscous posteriorly. Tegulae chestnut-brown but white dorsally. Legs white ringed with a mixture of fuscous and chestnut. **Forewings** shining orange-brown; a small white median dash at base, dark edged

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FIG. 4. ♂ Genitalia: **4a,** ventro-lateral view of *Acrocercops pectinivalva* n. sp.; **4b,** lateral view with right valve removed, valve and aedoeagus (enlargement of tip × 2) of *A. fuscapica* n. sp.; **4c,** dorso-lateral view of *Spulerina quadrifasciata* n. sp. with enlargement of comb.
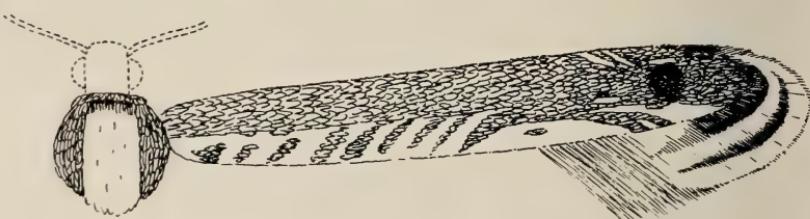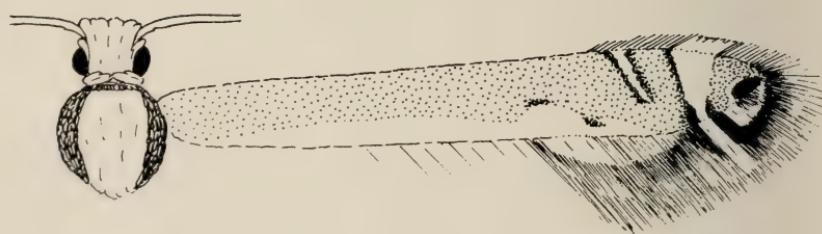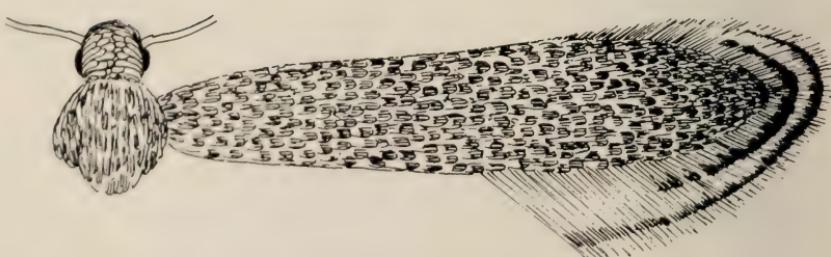
FIG. 5. Head, thorax and forewing pattern of those species not previously illustrated. **5a,** *Acrocercops leucostega;* **5b,** *A. rhothiastis;* **5c,** *A. siphonaula;* **5d,** *Cryphiomystis chalybophanes.* All drawn from holotypes in the British Museum (Natural History), London. (Not to scale).

dorsally; three dark-edged white fasciae at ¼, ½ and ¾ of dorsum; first fascia outwardly curved from dorsum, tapering to become almost obsolete at costa; second fascia, broadest on dorsum, slightly outwardly oblique from dorsum and markedly constricted just before costa; third fascia completely constricted to form two triangles—the smaller one on the costa; apical area chestnut-brown with a few scattered fuscous scales and a small whitish patch costally; apical cilia chestnut-brown. Hindwings and cilia fuscous.

Female genitalia (see Fig. 2c). Papillae anales moderate, rounded and finely haired; apophyses posteriores moderate, slightly sinuate; apophyses anteriores same length as apophyses posteriores, slender, straight and tapering; antrum sclerotized, short and cylindrical; ductus bursae and bursa copulatrix membranous and without signum [Genitalia, BM(NH) slide 21279].

Type specimens. Holotype ♀ only. Ile-Ife, NIGERIA. 30.XII.1971, J. T. Medler. Type in the British Museum (Natural History), London.

Remarks. Closely related and superficially similar to *Phyllonorycter loxozana* (Meyrick, 1936) n. comb. (transferred from *Lithocolletis*), from which it can be easily separated by the shorter and more sclerotized antrum of the ♀ genitalia and the constricted second fascia of the forewings.

These additions and new records bring the West African Gracillariidae to 16 known species. The following list gives these species, the location of illustrations of wing pattern and genitalia, and their known distribution:

Ectropina sclerochitoni Vári, 1961
  (Wing, ♂ gen., ♀ gen. in Vári (1961), Pl. 5, fig. 2, Pl. 54, fig. 2, Pl. 81, fig. 5) Nigeria.
Epicephala suttoni n. sp.
  (Wing, Fig. 1a; ♀ gen. Fig. 2a) Nigeria.
Aristaea onychota (Meyrick, 1908)
  (Wing, ♂ gen., ♀ gen. in Vári (1961), Pl. 4, fig. 7, Pl. 55, fig. 2, Pl. 84, fig. 2) São Tomé, Nigeria.
Stomphastis conflua (Meyrick, 1914)
  (Wing in Vári (1961), Pl. 9, fig. 2; ♂ gen., Fig. 3a; ♀ gen., Fig. 2b) Nigeria.
S. thaustica (Meyrick, 1908) [=*plectica* Meyrick, 1912]
  (Wing, ♂ gen., ♀ gen. in Vári (1961), Pl. 6, fig. 5, Pl. 46, fig. 6, Pl. 87, fig. 2) Ghana.
Lamprolectica apicistrigata (Walsingham, 1891)
  (Wing, ♂ gen., ♀ gen in Vári (1961), Pl. 15, fig. 5, Pl. 60, fig. 3, Pl. 84, fig. 4) Gambia, Nigeria.
Acrocercops bifasciata (Walsingham, 1891)
  (Wing in Walsingham (1891), Pl. vi, fig. 68; ♂ gen. Fig. 3c) Gambia, Nigeria.
A. fuscapica n. sp.
  (Wing & ♂ gen., Fig. 1c, 4b) Nigeria.
A. leucostega (Meyrick, 1932) n. comb. Originally described as *Tinea leucostega* but transferred to Gracillariidae by Gozmány & Vári (1973).
  Placement in *Acrocercops* is tentative as the unique holotype is without abdomen.
  (Wing, Fig. 5a) Sierra Leone.
A. pectinivalva n. sp.
  (Wing & ♂ gen., Fig. 1b, 4a) Nigeria.
A. rhothiastis Meyrick, 1921. Only holotype known and it is without abdomen.
  (Wing, Fig. 5b) Nigeria.
A. siphonaula Meyrick, 1931
  (Wing, ♂ gen., ♀ gen., Fig. 5c, 6a, 6b) Sierra Leone.
Spulerina hexalocha (Meyrick, 1912)
  (Wing in Vári (1961), Pl. 21, fig. 6) Sierra Leone.
S. quadrifasciata n. sp.
  (Wing & ♂ gen., Fig. 1d, 4c) Nigeria.

6a

6b

6c

circa 0·1mm
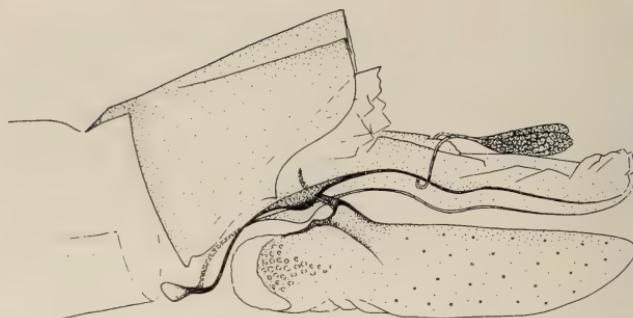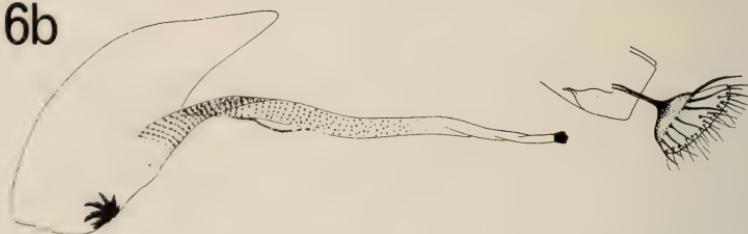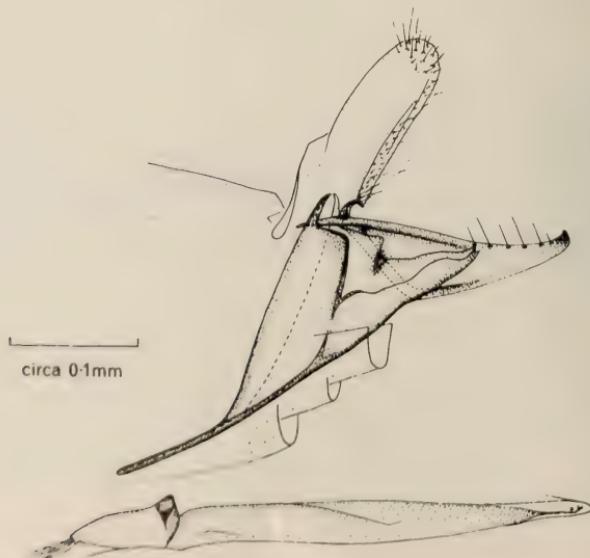
Cryphiomystis aletreuta (Meyrick, 1936) [=*chalybophanes* (Meyrick, 1937)]
   (Wing & ♂ gen., Fig. 5d, 6c) Nigeria.
Phyllonorycter caudasimplex n. sp.
   (Wing & ♀ gen., Fig. 1e, 2c) Nigeria.

These species probably represent not more than 10% of the West African gracillariid fauna.

ACKNOWLEDGMENTS

LITERATURE CITED

GOZMÁNY, L. A. & L. VÁRI. 1973. The Tineidae of the Ethiopian Region. Transvaal Museum, Pretoria. (Memoir No. 18).
THISELTON-DYER, W. T. 1913. Flora of Tropical Africa. Vol. VI, Sect. 1. Lovell Reeve, London.
VÁRI, L. 1961. South African Lepidoptera. Vol. I. Lithocolletidae. Transvaal Museum, Pretoria. (Memoir No. 12).
WALSINGHAM, LORD. 1891. Transactions of the Entomological Society of London for 1891, p. 63–132.

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FIG. 6.   ♂ & ♀ Genitalia not previously illustrated: **6a,** lateral view of ♂ genitalia of *Acrocercops siphonaula* with left valve removed and aedoeagus shown separately [Holotype, BM(NH) Slide 6083]; **6b,** lateral view of ♀ genitalia of *A. siphonaula* [Allotype, BM(NH) Slide 16039]; **6c,** lateral view of ♂ genitalia of *Cryphiomystis chalybophanes* with left valve removed and aedoeagus shown separately [Holotype, BM(NH) Slide 6082].

NOTES ON THE BEHAVIORAL ECOLOGY OF *PERRHYBRIS LYPERA* (PIERIDAE) IN NORTHEASTERN COSTA RICA

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ABSTRACT. *Perrhybris lypera* (Pieridae: Pierinae: Pierini) occurs in low adult densities in lowland tropical rain forests of Central America and northern South America. Females possess the "tiger stripe" coloration known for many classically unpalatable Neotropical butterflies and their mimics, while males resemble "whites." These differences are related to sex-limited behavioral patterns. Adult behavior, including oviposition and differences in local abundance between males and females, and certain features of juvenile behavior (larval foodplant, behavior of first instar larvae, and pupation) were studied in northeastern Costa Rica. A cluster of 18 healthy pupae of *P. lypera* was discovered on a leaf of the forest understory tree *Ocotea* sp. (Lauraceae) and produced a 1:1 sex ratio of adults. Lengthy cluster oviposition on *Ocotea* results in bright yellow eggs being deposited in rows on the upper sides of young leaves amidst dense stellate pubescence. Prior to oviposition, considerable time is spent by the females "inspecting" the foodplant. Egg hatchability and survival for over the first three days in the wild was 100%. The egg stage lasted 16 days and the first instar larvae were gregarious. They partially devoured their egg shells and commenced communal feeding on soft leaf tissue. Adult females (presumably mated) occurred in low numbers near larval foodplants (trees), while solitary males were seldom seen. Aggregations of fresh males observed near breeding sites might have been leks, functioning to attract unmated females. Gregarious larval behavior and pupation result from cluster oviposition. They seem to facilitate aggregative behavior in male *P. lypera*.

The purpose of this paper is to report some interesting features of the behavioral ecology of adults and first instar larvae of the Neotropical pierid *Perrhybris lypera lypera* (Kollar) in northeastern Costa Rica. Perhaps owing to the small number of species of this South American genus (Seitz, 1924), and the rather secretive habits of the females in primary forest understories, little is known about the biology of *Perrhybris*. With the exception of the closely-related *P. pyrrha* Fabricius in Brazil (Prittwitz, 1965; D'Almeida, 1921, 1922), *Perrhybris* have not been extensively studied. Virtually nothing is known about the larval foodplants of *P. lypera* and the behavior of adults and larvae. This paper is mainly observational and is not an attempt to describe the detailed morphology of the early stages of *P. lypera*.

STUDY AREAS AND METHODS

Perrhybris lypera was briefly studied during 1969 at Finca La Selva, near Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica (elev. 98 m), a zone of relatively undisturbed Lowland Tropical Wet Forest (Holdridge, 1967). A collection of gregarious pupae was made from a presumed larval foodplant, and male behavior was observed.

More extensive studies of *P. lypera* were subsequently conducted at Finca La Tigra, near La Virgen de Sarapiqui (elev. 200 m) in a zone of relatively disturbed Premontane Tropical Wet Forest; these additional studies were done in February 1977, August 1977, and August 1978. These studies focused on identification of a larval foodplant, and observations of adult behavior (including oviposition), and larval behavior. Female specimens from La Selva and La Tigra match *P. lypera lypera* from Puerto Viejo, in the Allyn Museum of Entomology, as do male specimens from Guatemala and Ecuador.

At Finca La Selva, a cluster of 18 gregarious, clearly pierid pupae was found on an attached leaf of a primary forest understory tree (canopy about 4 m) and they were kept until eclosion to identify the species and sex ratio. A voucher specimen of leaves from the tree was kept for identification. On 1 February 1977, the oviposition behavior of one female *P. lypera* was studied for several hours. The eggs were collected for laboratory study a few days later. A section of the branch bearing the leaf with eggs was placed in a clear plastic bag and kept tightly sealed except for examinations. The number of eggs, their size, shape, and color were recorded; developmental time for the eggs also was estimated and the first instar larvae were examined for resting, locomotion, and feeding behavior. The study of both eggs and larvae lasted 28 days.

During the same period at Finca La Tigra, other individuals of the same tree species used by *P. lypera* for oviposition were located and the activity of adult *P. lypera* at these trees was observed. Additional voucher specimens of the leaves of these trees were collected. During later study periods (1–4 August 1977 and 3–5 August 1978), adult behavior of *P. lypera* was studied further. Of interest was the re-occurrence of adults in the same patches of forest understory for the three widely-spaced study periods at Finca La Tigra. Further observations were made on oviposition behavior by a single individual (August 1977), and inter-female interactions were noted at larval foodplant trees. The abundance and locations of males and females also were recorded.

RESULTS

Pupation Behavior and Sex Ratio

The 16 pupae produced eight females and eight males of *P. lypera*. These eclosed between 0630–0730 h. The striking sexual dimorphism of this medium-sized butterfly has been described (Seitz, 1924). Little variation between individuals of each sex was found in the adults obtained from this aggregation of pupae. The fully-sclerotized pupae
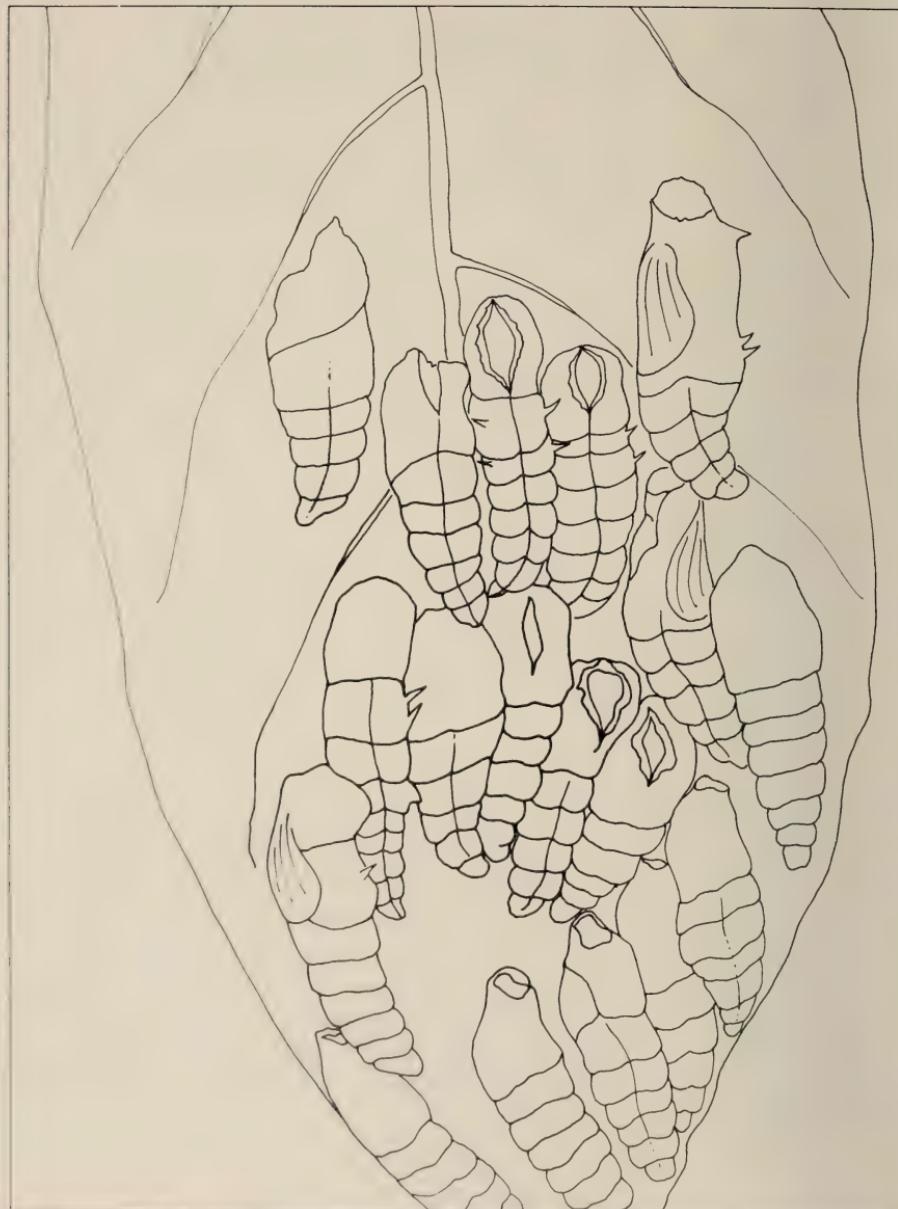
FIG. 1. An aggregation of pupae of *Perrhybris lypera* on a mature leaf of *Ocotea* (Lauraceae), discovered at Finca La Selva. This drawing was made from a poor-quality black-and-white photograph of the pupal cases after eclosion.

were orange-brown. They were spaced tightly together on the underside of the distal-half of a mature leaf of *Ocotea* (Fig. 1). The pupae were positioned in an orderly fashion such that they all faced the same direction, with heads toward the leaf's petiole. The pupae were oriented upward and were inconspicuous in heavily-shaded forest understory.

Oviposition Behavior and Larval Foodplant

During the first instance of oviposition a single *P. lypera* was observed on 1 February 1977 at 1100 h. The butterfly fluttered around and through the five meter canopy of the larval foodplant (tree) for 63 min before landing on a young leaf to initiate egg-laying. The tree was in an opening within mixed advanced secondary and primary tropical rain forest. The leaves were brightly flecked with sunlight, making it possible to watch the butterfly flutter about the tree. Many light green young leaves were located near the top of the tree, clustered in threes and fours at the tip of a branch. Having alighted, the butterfly folded its wings and remained in that position until oviposition was completed [despite having a hummingbird (species unidentified) land on a nearby branch of the same tree (about 0.33 m away) and stay there for about 10 min, before flying away]. Even with binoculars, it was difficult to observe the resting butterfly from the ground, so I climbed up on some large limbs of a recently fallen tree to observe it more closely.

The butterfly remained on the leaf until 1750 h that day, indicating that oviposition lasted more than 5 hours. Periodically checking, I could just make out a raft of brilliant yellow eggs behind the butterfly. The butterfly was positioned with its head toward the leaf petiole and the raft of yellow eggs was located near the distal tip of the leaf (Fig. 2). During oviposition, the weather was intermittently sunny and overcast but these changes did not interrupt oviposition. The tree was examined each of the following three days for the presence of *P. lypera* but none was spotted. The raft of eggs was collected on the fourth day. Species determination of the tree was not possible owing to a lack of flowers and fruit. At the study site *Ocotea* is distributed as single trees (3–5 m tall), each having a dense canopy (Fig. 3). Seven trees were found within an area about 275 m², with distances between trees ranging from 20–80 m.

There were a total of 44 oblong (spindle-shaped) yellow eggs in the raft, and all but two were affixed to the young leaf in neat rows (Fig. 2). Each was securely fastened to the leaf even though the young leaf was very pubescent, a condition considerably less apparent in mature leaves of *Ocotea* (Lawrence, 1951).

FIG. 2. Egg and larval aggregations of *P. lypera*. Clockwise from upper right: eggs on upper side of a young leaf of *Ocotea*, and first instar larvae devouring egg shells. Note that the pronounced stellate pubescence is evident in all four photographs.

FIG. 3. The canopy leaves of *Ocotea,* a tropical rain forest understory tree that is a larval food plant of *P. lypera* in northeastern Costa Rica.

Behavior of First Instar Larvae

The eggs hatched in 16 days without noticeable color changes. Hatching (Fig. 2) took place over a 26-hour period. The first instar larvae of *P. lypera* were 2.5 mm long with shiny black head capsules and striped lemon-yellow setae-covered bodies. They partially devoured their emptied egg shells. There was no cannibalism. Egg hatchability and survivorship for 3.5 days in the wild, and 12.5 subsequent days in the laboratory, was 100%. Within 2 days after hatching, the larvae became dark green and were speckled with yellow flecks. Feeding was done synchronously by the group, and was initiated at the edge of the same leaf where the larvae hatched, but on the underside. (Larvae were not reared beyond the first instar, because I had to leave the study area at this time.)

Behavior of Adults

During 16 days of observing adult *P. lypera* in the same general area a total of 28 sightings of females took place. With the exception of a second instance of oviposition (described below), these sightings consisted of seeing individual females flying through the understory,

generally 4–6 m above the ground. Two females were observed fluttering around an individual *Ocotea* about 40 m from the one where oviposition was first studied; the second tree was about the same size as the first. On this particular morning (11 August 1977) one female was observed to alight on a young leaf near the top of the tree and to imitate oviposition. Within 20 min, a second female appeared at the tree and repeatedly flew around the first female, as if attempting to land on the same leaf. A total of 7 attempted landings were made within a 10-min period. After 25 min, the second female dislodged the first one and began ovipositing on the same leaf.

While males were absent from the forest understory where females were observed, an aggregation of 12 fresh males of *P. lypera* was accidentally flushed from understory vegetation one morning (13 August 1977) about 25 m from where oviposition was first observed. No females were present. The males had been resting on a small tree. All appeared to be recently eclosed. Although considerable searching was done on several dates, solitary males were not found in the area. During April 1970 at Finca La Selva, eight groups (ranging from six to 20 adults) of freshly eclosed males were seen.

DISCUSSION AND CONCLUSIONS

Perrhybris lypera occurs in the understory of tropical rain forest in Costa Rica and is seldom seen in other habitat. The larval foodplant, *Ocotea*, is a solitary member of the forest understory. Ehrlich and Raven (1965) discuss the larval foodplant families for the Pierinae. Jorgenson (1916) mentions finding a large aggregation of larvae and pupae of *Pereute* on the trunk of *Ocotea spectabilis*. There is also one record of *Pereute* feeding on Tiliaceae (Biezanko, 1959). Both *Pereute* and *Perrhybris* belong to the Pierinae (Ehrlich, 1958) and the present discovery of *Perrhybris* feeding on *Ocotea* represents a second record for lauraceous-feeding within this subfamily and tribe. J. Röber in Seitz (1924) mentions that Brazilian *P. pyrrha* females are found in forest habitats, while males appear to frequent various kinds of moist patches of ground. The Costa Rican observations indicate that *P. lypera* breeds in the understory layer of lowland tropical rain forests. The present-day clearance of forest habitats in northeastern Costa Rica may result in the local extinction of this species.

Males of *Perrhybris*, *Pereute*, and *Archonias* (all Pierini) exhibit gregarious behavior when imbibing moisture from the ground (Seitz, 1924); less is known about the behavioral habits of the immature stages, although Röber mentions that probably the larvae of *A. bellona* Cramer are gregarious. *Perrhybris* deposits eggs singly or in clusters on the undersides of leaves (Prittwitz, 1865; D'Almeida, 1921). *Ar-*

chonias tereas approximata Butler exhibits cluster oviposition and
larval gregariousness in the mountains of central Costa Rica (Young,
pers. obs.). Lee D. Miller (pers. comm.) pointed out that *Archonias*
and *Pereute* are very closely related genera. These three genera and
a few others (Seitz, 1924) exhibit gregarious behavior generally not
seen in other genera of the Pierini. For example, the Neotropical
Itaballia (Pierini) and *Dismorphia* (Dismorphinae) exhibit single
oviposition, even though a female may deposit several eggs on the
same individual foodplant during one visit (Young, 1972a, b). In *Per-
rhybris*, gregarious behavior is evident in the larvae and pupae, a
consequence of cluster oviposition. Adults of either sex also may be
gregarious. Gregariousness of larvae is well known in several other
pierid genera, although the evolutionary origin of this behavior is
unknown.

Most aposematically-colored insects are equipped with powerful
chemical defenses. They often form conspicuous aggregations of in-
dividuals (Cott, 1957). Vertebrate predators quickly learn to avoid
them, presumably because of the vivid coloration which is reinforced
by the gregarious behavior (Brower & Brower, 1964; Eisner, 1970).
In some species of *Nymphalis* (Nymphalidae) with gregarious larvae,
solitary larvae are discovered and are eaten more quickly than indi-
viduals in groups (Mosebach-Pukowski, 1937). In *Perrhybris*, the gre-
garious habits of larvae and pupae are probably protective, as well.
The leaves of *Ocotea* contain highly odorous oils, in addition to a
myristic aldehyde and a sesquiterpene (Uphof, 1925). These second-
ary compounds become effective chemical defenses in some insects
(Eisner, 1970), and they are sometimes obtained from foodplants (Eis-
ner & Meinwald, 1965). The gregarious yellow and green speckled
larvae and aggregated reddish-orange pupae suggest aposematic col-
oration and behavior, as does the coloration of the adult females. The
closely related *P. pyrrha* is considered a classic example of sex-lim-
ited Batesian mimicry, yet the information reported here for *P. lypera*
suggests that these butterflies are unpalatable. The crucial evidence,
namely the ability of the larvae to sequester noxious secondary com-
pounds, is lacking and warrants study. The problem becomes complex
when a species feeds on more than one foodplant, since lepidopteran
larvae can switch between palatable and unpalatable properties de-
pending upon the foodplant (Rothschild et al., 1979). The vivid yellow
aggregated eggs of *P. lypera* are not mimicking any extrafloral nec-
taries of *Ocotea*, as are the eggs of some species of *Heliconius* but-
terflies (Nymphalidae: Heliconiinae) on their larval foodplants, Pas-
sifloraceae (Benson et al., 1976), but perhaps they are protected from
egg predators such as ants, by being positioned in a dense matting of

stellate pubescence on young leaves. As seen for *Mechanitis* (Nymphalidae: Ithomiinae) (Young & Moffett, 1979), such egg clusters may be so protected before group related chemical defenses arise in the larval stage.

Perrhybris lypera exhibits considerable oviposition site-selection. The relatively long period of surveying the larval foodplant before laying eggs, the selection of young leaves for egg-laying, and the apparent displacement behavior of one ovipositing female by another female indicate a highly selective or specialized form of oviposition. Butterflies and other insects that deposit large quantities of eggs on a single leaf may exhibit such behavior as an adaptive response to insuring the survival of their progeny. However, such behavior may have certain advantages for the female butterfly herself. The sedentary behavior associated with the slow and careful deposition of many eggs at a single spot in the environment could be considered as a "low risk" activity for the female (Maynard Smith, 1978), in that the stationary insect is concealed from predators which might otherwise eat it before the eggs are deposited. Even aposematically-colored butterflies are eaten by predators such as birds (Calvert et al., 1979). Such behavior may be most adaptive for butterfly species with restricted daily activity. *Perrhybris* females are found in the same patch of forest understory over long periods, suggesting that mated females tend to stay near foodplants. If larval foodplant patches are relatively scarce over extensive areas of habitat, this could be an additional factor selecting for cluster oviposition.

The preciseness of selecting young leaves of *Ocotea* probably allows the young larvae to feed successfully on soft tissues. In some *Papilio* (Papilionidae) females can distinguish young and old leaves of the foodplant based on color differences in the leaves (Vaidya, 1969). The stellate pubescence of the leaves is not a deterrent to egg deposition or feeding of young larvae. In another plant-herbivore interaction, namely *Mechanitis isthmia* and various Solanaceae with dense coverings of stellate pubescence on leaves, communal feeding in the first and second instar larvae facilitates the breaking down and removal of the pubescence, which would otherwise be difficult for solitary larvae to penetrate (Young & Moffett, 1979). Communal feeding in the gregarious larvae of *P. lypera* may serve a similar function. Further detailed field studies are needed to determine the parameters of synchronous group activities in the larvae, such as resting, feeding, molting, and pupation.

The presence of female *P. lypera* at the same site at different times of the year indicates that breeding is probably continuous throughout the year, even though the region experiences a slight "veranillo" dur-

ing January and February. Understory habitats may be insulated to some degree from seasonal changes in rainfall. Ebert (1969) found that adult *Pereute antodyca* (Boisduval) and *P. swainsoni* (Gray) in highland rain forest in eastern Brazil are active throughout most of the year. In northeastern Costa Rica *Perrhybris* female densities in areas of forest where the larval foodplants occur are generally low (from 1–5 individuals are seen on a given day at one area). The absence of a similar distribution of males is behavioral, since egg clusters produce a 1:1 sex ratio, assuming that the pupal data are typical for a population.

Synchronous eclosion of both sexes in a cluster of pupae permits mating to take place quickly, and, once completed, females disperse in search of oviposition sites. Such male aggregations are different from the well known cases of male pierids aggregating at mud puddles. Freshly-eclosed *Perrhybris* males aggregate on forest understory plants where they are not engaged in feeding. Perhaps such aggregations function to facilitate courtship in a manner analogous to the well-documented cases of lek behavior in some vertebrates (e.g., Downhower & Armitage, 1971). Further studies are needed to examine the function of male aggregations in *Perrhybris*, their locations in relation to preparation sites, and the prediction that recently-mated females rapidly disperse from places of high male density as they search for larval foodplants with patchy distributions. Under such a breeding system, the striking sexual dimorphism in wing coloration in *P. lypera* may accomplish several functions: in addition to reinforcing a warning of female unpalatability, and possible mimetic confusion for vertebrate predators, it may facilitate recognition of sex in the shaded forest understory where aggregations of males may serve as "whiteflags" for attracting unmated females.

ACKNOWLEDGMENTS

preparation of Fig. 1. One of the reviewers pointed out the helpful Jorgenson reference.

LITERATURE CITED

BENSON, W. W., K. S. BROWN, JR. & L. E. GILBERT. 1976. Coevolution of plants and herbivores: passion flower butterflies. Evolution 29: 659–680.

BIEZANKO, C. M. 1959. Pieridae de zona missioneira do Rio Grande do Sul. Arq. Entomol., Ser. B, Inst. Agron. do Sul, Pelotas, Brazil, 12 p.

BROWER, L. P. & J. V. Z. BROWER. 1964. Birds, butterflies, and plant poisons: a study in ecological chemistry. Zoologica 49: 137–159.

CALVERT, W. H., L. E. HEDRICK & L. P. BROWER. 1979. Mortality of the Monarch butterfly (*Danaus plexippus* L.): avian predation at five overwintering sites in Mexico. Science 204: 847–850.

COTT, H. B. 1957. Adaptive Coloration in Animals. Metheun, London, 508 p.

D'ALMEIDA, R. F. 1921. Notes sur quelques Lepidopteres d'Amerique du Sud. Ann. Entomol. Soc. France 90: 57–65.

———. 1922. Melanges Lepidopterologiques. Berlin, 46 p.

DOWNHOWER, J. F. & K. B. ARMITAGE. 1971. The yellow-bellied marmot and the evolution of polygamy. Amer. Natur. 105: 355–370.

EBERT, H. 1969. On the frequency of butterflies in eastern Brazil, with a list of the butterfly fauna of Pocos de Caldas, Minas Gerais. J. Lepid. Soc. 23, Suppl. No. 3. 48 p.

EHRLICH, P. R. 1958. The comparative morphology, phylogeny and higher classification of the butterflies (Lepidoptera: Papilionoidea). Univ. Kansas Sci. Bull. 39: 307–370.

——— & P. H. RAVEN. 1965. Butterflies and plants: a study in coevolution. Evolution 18: 586–608.

EISNER, T. 1970. Chemical defense against predation in arthropods. *In* E. Sondheimer and J. B. Simeone, eds., Chemical Ecology, pp. 157–217, Academic Press, New York. 365 p.

——— & Y. C. MEINWALD. 1965. Defensive secretion of a caterpillar (*Papilio*). Science 150: 1733–1735.

HOLDRIDGE, L. R. 1967. Life zone ecology. Trop. Sci. Center, San Jose, Costa Rica. 89 p.

JORGENSEN, P. 1916. Las mariposas Argentinas: familia Pieridae. Anales del Museo Nacional Hist. Natural de Buenos Aires 28: 427–520.

KLOTS, A. B. 1933. A generic revision of the Pieridae (Lepidoptera). Entomol. Amer. 12: 139–242.

LAWRENCE, G. H. M. 1951. Taxonomy of the vascular plants. MacMillan Co., New York. 823 p.

MAYNARD SMITH, J. 1978. Optimization theory in evolution. Ann. Rev. Ecol. Syst. 9: 31–56.

MOSEBACH-PUKOWSKI, E. 1937. Uber die Raupengesellschaften von *Vanesso io* und *vanessa urticae*. Zeitschr. Morphol. Okologie Tiere 33: 358–380.

PRITTWITZ, O. 1865. Beitrag zur fauna des Corcovedo. Stett. Ent. Ztg. 26: 123–143.

ROTHSCHILD, M., R. APLIN, J. BAKER & N. MARSH. 1979. Toxicity induced in the tobacco horn-worm (*Manduca sexta* L.) (Sphingidae, Lepidoptera). Nature 280: 487–488.

SEITZ, A. (ed.) 1924. Macrolepidoptera of the world. Vol. 5. The American Rhopalocera, Pt. 1, A. Kernan Verlag, Stuttgart. 615 p.

UPHOF, J. C. T. 1925. Malas hierbas de Cuba. Revista Agr. Com. y Trab. Cuba 7: 5–13.

VAIDYA, V. G. 1969. Investigations on the role of visual stimuli in the egg-laying and resting behaviour of *Papilio demoleus* L. (Papillionidae, Lepidoptera). Anim. Behav. 17: 350–355.

YOUNG, A. M. 1972a. A contribution to the biology of *Itaballia caesia* (Lepidoptera: Pieridae) in a Costa Rican mountain ravine. Wasmann J. Biol. 30: 43–70.
———. 1972b. Notes on the life cycle and natural history of *Dismorphia virgo* (Pieridae: Dismorphiinae) in Costa Rica. Psyche 79: 165–178.
——— & M. W. MOFFETT. 1979. Studies on the population biology of the tropical butterfly *Mechanitis isthmia* in Costa Rica. Amer. Midl. Natur. 101: 309–319.

NOTES ON THE TYPE AND TYPE COLLECTOR OF
PARNASSIUS BEHRII (PAPILIONIDAE)

Parnassius behrii was described by W. H. Edwards (1870, Trans. Amer. Entomol. Soc. 3: 11) from a California specimen that he had received from H. H. Behr. In his treatment of the types of butterflies named by W. H. Edwards, F. M. Brown (1975, Trans. Amer. Entomol. Soc. 101: 1–31) gives the type locality of *Parnassius behrii* as "near the summit of Mt. Lyell, Yosemite Valley, California" and cites J. W. [sic M.] Hutchings as the collector. Brown relied on Henry Edwards (1878, Proc. Cal. Acad. Sci. 11–14) for this information. On p. 12 Edwards stated that "*P. behrii* was taken by Mr. J. W. [sic] Hutchings, formerly of Yosemite Valley, near the top of Mt. Lyell, at an altitude of nearly 11,000 ft." On p. 13, he further relates that the type of *behrii* was taken by Mr. Hutchings.

This information is in error. J. M. Hutchings could not have collected the types of *P. behrii* on Mount Lyell. Hutchings (see accompanying note, J. Lepid. Soc. 34: 68) lived in Yosemite Valley from 1862 until 1902. He reported on his climb of Mount Lyell in his book (Hutchings, 1886, In the Heart of the Sierras, priv. publ.), and while he does not give the dates of his climb, he states that the climb was inspired by John Muir's report of a "live glacier" on Mount Lyell. He further states that he found the card of a Mr. Tileston on the summit some ten days after it had been left. This information is a bit conflicting as Muir (1872, Overland Monthly, Dec.) indicated that he discovered the glacier in October 1871. Tileston (1922, Letters of John Boies Tileston, Boston, privately printed) wrote that he reached the summit "on Monday the 28th August, 1871." Possibly Hutchings mistook the date on Tileston's card, but in either case, he did not make the climb before late in the summer of 1871 and even more likely before the summer of 1872. Edwards had described *Parnassius behrii* in January or February of 1870.

While Hutchings could have collected the types of *P. behrii*, he could not have collected them on Mt. Lyell. He undoubtedly did, however, collect the specimens that came into the hands of Henry Edwards. It is much more likely that the types of *P. behrii* were collected by members of the California State Geological Survey, who supplied Behr with most of his "High Sierra" materials, during the summers of 1863 or 1864. W. H. Brewer and C. F. Hoffman, of the Survey, were the first to climb Mount Lyell, the mountain which they discovered and named, on 2 July 1863.

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A NEW *PAROCHROMOLOPIS* (EPERMENIIDAE) FROM COSTA RICA

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ABSTRACT. *Parochromolopis psittacanthus*, new species, is described from specimens reared from fruits of *Psittacanthus calyculatus* A. Don (Loranthaceae) in Costa Rica.

Biological studies by Dr. D. H. Janzen (University of Pennsylvania) in Costa Rica have involved the rearing of an undescribed species of Epermeniidae (Cupromorphoidea) of the genus *Parochromolopis*. The description of the moth follows so a name will be available for publication of the bionomics of the species.

Parochromolopis psittacanthus, new species

Description. Size, 4.0–4.6 mm forewing length. **Head:** fuscous, speckled with black and dull white. Labial palpus large, porrect, brown speckled with black and dull white, tufted dorsally on middle segment. Antenna with scape flattened, same coloration as head. **Thorax:** same coloration as head. Venter pale tan. Legs fuscous speckled with brown and tan. Forewing (Fig. 1) tan with black-tipped scales basally between veins and margins, as 4 tufts along dorsal margin, and inward by each tuft, and as 3 spots at mid-wing, end of cell, on distal ¼ and subapically. Brown scales between black-tipped scales from mid-wing to apex. Venter fuscous. Hindwing gray fuscous;

Fig. 1. *Parochromolopis psittacanthus* Heppner, n. sp., paratype ♀.
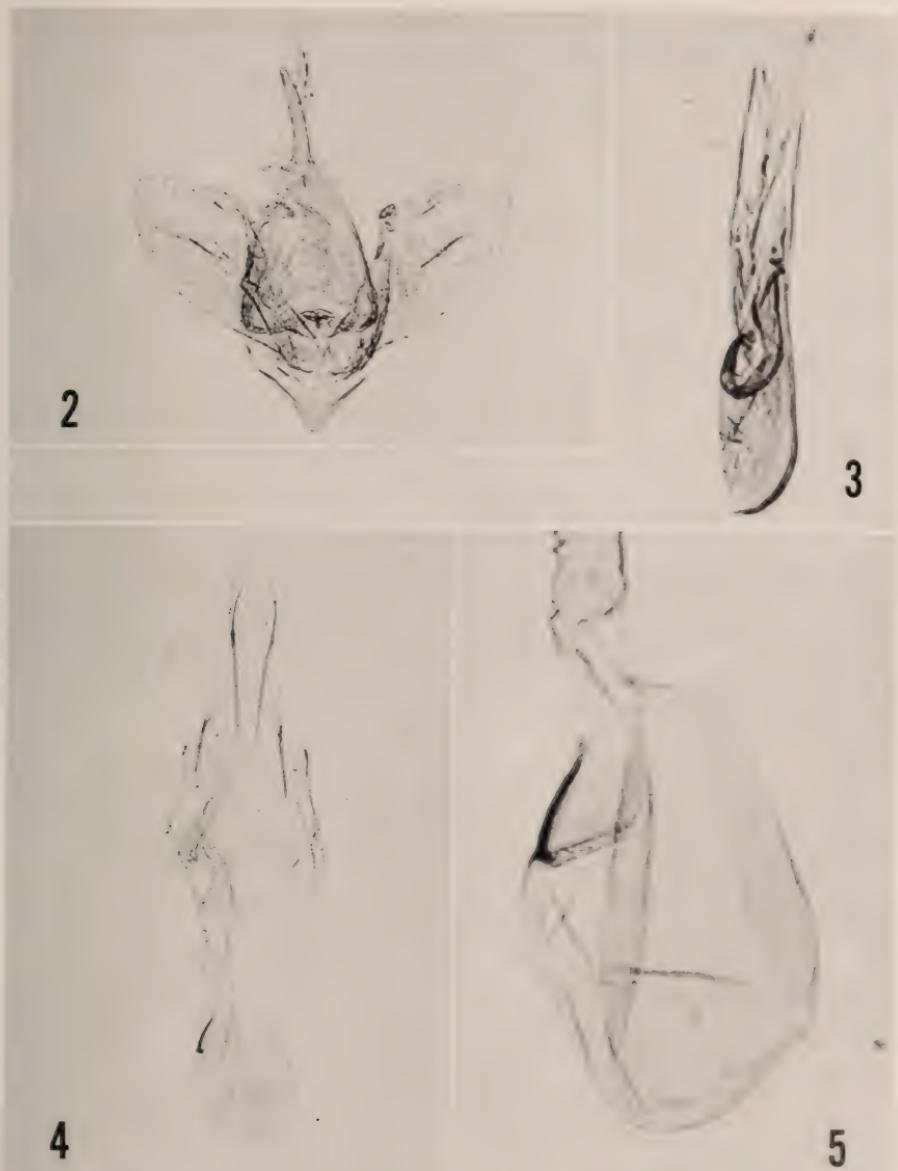
FIG. 2–5. *P. psittacanthus* Heppner, n. sp.: 2, holotype ♂ (slide USNM 77837); 3, aedeagus holotype ♂ (enlarged); 4, paratype ♀ (slide USNM 77836); 5, signum, paratype ♀ (enlarged).

venter fuscous. **Abdomen:** fuscous. Male genitalia as in Fig. 2: uncus long, narrow; tegumen as large as valva; vinculum with small triangular saccus; valva simple setaceous, with apex rounded but slightly oblique; dorsal margin of valva with twisted setaceous hook. Aedeagus subequal to distance from tip of uncus to saccus; cornutus a large recurved hook-like spine (Fig. 3). Female genitalia as in Fig. 4: ovipositor normal; posterior apophyses twice as long as anterior pair; ostium bursae small, membranous and merging into ductus bursae, which is membranous; bursa copulatrix elongate-ovate, with a spicule patch edged by a V-shaped keel-like signum (Fig. 5).

Type.   Holotype ♂: Santa Rosa Natl. Park, Guanacaste Prov., Costa Rica, emerged Jan 1979 ex fruits *Psittacanthus calyculatus,* D. H. Janzen (USNM Type No. 76271).

Paratypes.   8♀, same data as holotype. (Paratypes to British Museum (Natural History) and Zoologisches Museum, Humboldt Univ., Berlin, DDR.; and USNM.)

Biology.   The larvae are borers in the fruits of the host plant, *Psittacanthus calyculatus* A. Don (Loranthaceae), a tropical mistletoe. D. H. Janzen is describing the life history of the species in more detail in a separate paper.

Remarks.   This species is superficially very similar to *Parochromolopis floridana* Gaedike from Florida, but the genitalia distinguish the two species. In *P. psittacanthus* there is no basal appendage on the valva as in *P. floridana,* the cornutus is larger, and in the female the keel-like signum is larger than in *P. floridana.* The two species appear to be very closely related but the male genitalia of *P. psittacanthus* actually have the valva and aedeagus more similar to *Parochromolopis parishi* Gaedike from Peru. The Peruvian species has the valva more quadrately blunt distally than in *P. psittacanthus* and the twisted appendage of the valva is somewhat longer.

The genus *Parochromolopis* was only recently described (Gaedike, 1977) for three species, one from southern Florida and two from Peru. *Parochromolopis psittacanthus* is the first epermeniid known from Central America. Various epermeniids are known to be borers of buds, fruits, seeds or are leaf miners as larvae, so the biology of *P. psittacanthus* conforms to the family characteristics. The host plant is the first record of the plant family Loranthaceae for the Epermeniidae.

Literature Cited

Gaedike, R. 1977. Revision der nearktischen und neotropischen Epermeniidae (Lepidoptera). Beitr. Ent. (Berlin), 27: 301–312.

A MODULAR, TRANSPORTABLE HABITAT SYSTEM FOR COLONIZATION OF GIANT SILKWORM MOTHS (SATURNIIDAE)

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ABSTRACT. A modular, transportable habitat system for indoor colonization of giant silkworm moths is described. The system is comprised of a series of single-purpose and multi-purpose components that can be assembled to provide the habitats necessary for the various life stages and life functions. The system is used primarily for maintaining laboratory colonies, but can be used for maintaining wild collected specimens in the field and for transporting specimens to and from the field and between laboratory locations.

We have used a variety of materials and methods to rear giant silkworm moths for research purposes. Because time and facilities are limited, we have made an effort to improve capability for rearing these moths by systematically identifying the equipment and methodology needed to provide habitats for the various life stages and life functions. This paper describes a modular, transportable habitat system that we have developed and used for the indoor colonization of giant silkworm moths. It represents a systematic incorporation of many of the commonly used methods that we, and other workers, have reported for achieving mating, insuring acceptable sex ratios in colonies, collecting fertile eggs, and transferring newly-hatched larvae to food plants (Collins & Weast, 1961, Crotch, 1956; Dirig, 1975; Miller & Cooper, 1976, 1977a, 1977b, 1980; Miller, 1978; Miller et al., 1977; Miller & Machotka, 1980; Taschenberg & Roelofs, 1970; Villiard, 1969; Waldbauer & Sternburg, 1973). The system is comprised of a series of single-purpose and multi-purpose components that are assembled to provide the necessary habitats. The system is transportable and can be used to maintain wild-collected specimens in the field and to transport specimens to and from the field and between laboratory locations. The modular system has been used to rear the following species: *Antheraea polyphemus* (Cramer); *Samia cynthia* (Drury); *Rothschildia forbesi* Benjamin; *Eupackardia calleta* (Westwood); *Hyalophora cecropia* (Linnaeus); *Hyalophora gloveri gloveri* (Strecker); *Hyalophora euryalis* (Boisduval); *Callosamia promethea* (Drury); *Callosamia angulifera* (Walker); and *Automeris io* (Fabricius).

Modular System Components

The components of the modular, transportable habitat system are made from inexpensive, readily available materials: metal coffee cans

TABLE 1. Summary of components used in the modular, transportable habitat system.

Component	Number of components used[1]		
	Small	Medium	Large
Water container	1	2	1
Mating container	1	0	1
Short tube	2	2	2
Long tube	1	1	1
Mating ring (small-mesh)	1	0	1
Mating ring (large-mesh)	0	0	1
Retaining ring	1	2	0
Coupling ring	1	1	1
Plant ring	2	2	2
Netting (small-mesh)	2	2	2
Netting (large-mesh)	2	2	2

* Oviposition bags, plastic liners, and paper liners are disposable components used in numbers as required.

and associated plastic lids; solder; wire screen; plastic tape, nylon netting; paper and plastic bags; and spray paint. The components are of three different diameters (small = 10 cm; medium = 13 cm; large = 15.5 cm) corresponding to the 1-, 2-, and 3-pound coffee cans. All metal surfaces are first sprayed with metal oxide primer; inner surfaces are sprayed with white gloss enamel to improve visibility, while outer surfaces are painted with various colors of enamel to code the components for easier identification.

The components of the modular system are summarized in Table 1 and illustrated in Figs. 1 and 2. Water containers and mating containers are single metal cans with one end removed. Water containers are used upright to hold water for the maintenance of food plant cuttings. Mating containers have a small ring soldered to the side to facilitate horizontal attachment to a tree or other structure. Mating containers may serve as water containers when necessary. Various sized tubes are used as containment structures for food plant cuttings or as supports for oviposition bags. Short tubes are single metal cans with both ends removed. Long tubes are two metal cans soldered together after both ends have been removed from each.

Retaining rings are plastic lids with the centers removed. They are used on top of the short and long tubes to hold netting materials in place. Mating rings consist of two plastic lids with the centers removed. Circular wire screens (small- or large-mesh) are placed be-

$\rightarrow$

FIG. 1   Components used to make two versions of the large larval rearing cage (tall).

MATING RING
(SMALL-MESH)

MATING RING
(LARGE-MESH)

SHORT TUBE

LONG TUBE

COUPLING RING

SHORT TUBE

PLANT RING

WATER
CONTAINER

MATING
CONTAINER
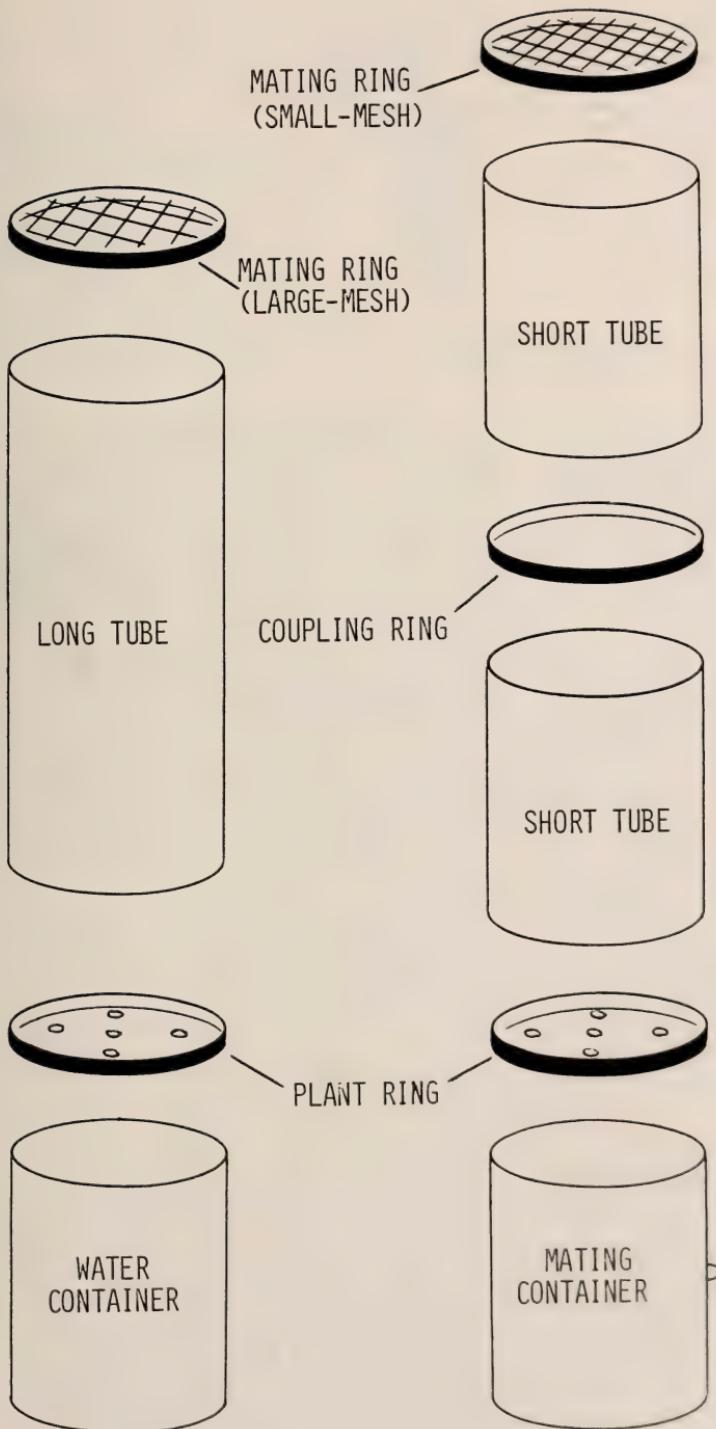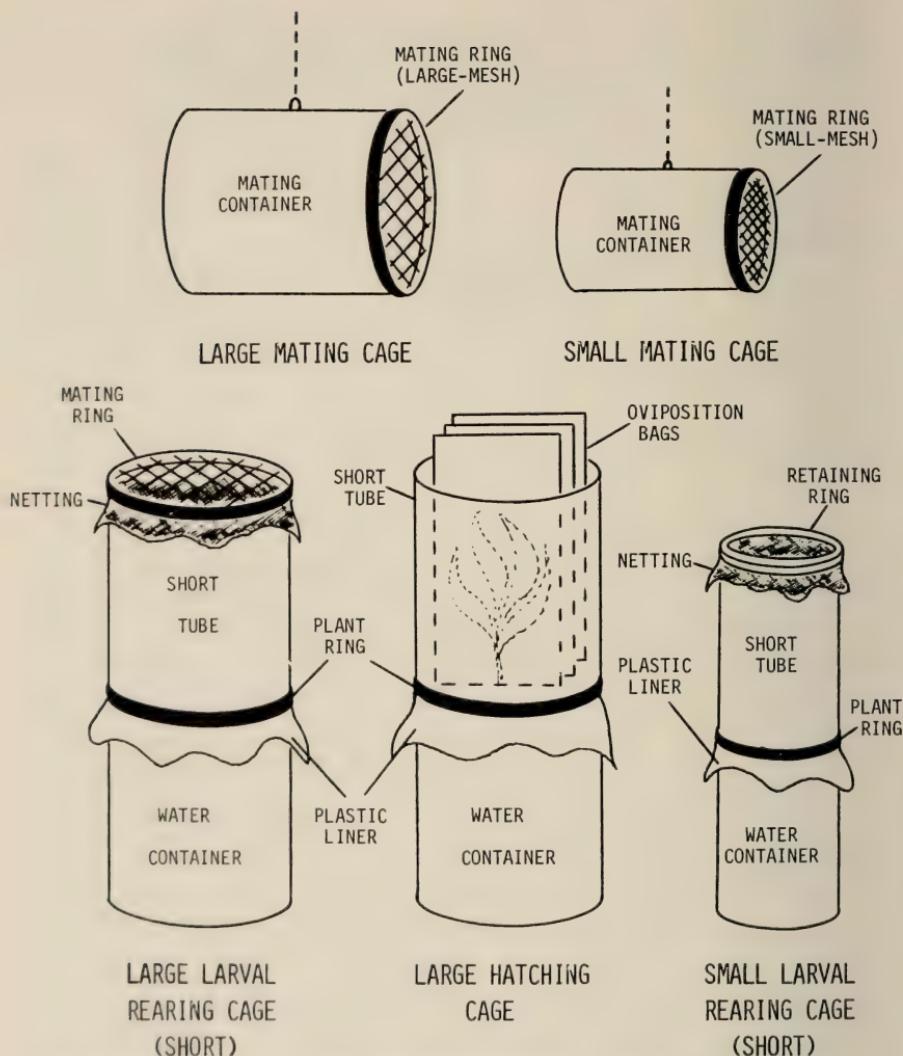
FIG. 2. Some typical configurations of the modular transportable habitat system.

tween the lids before they are placed together back to back and sealed around the outer edge with plastic tape. The small-mesh wire screens have diamond-shaped openings that are 1.27 cm on a side. The large-mesh wire screens have hexagonal openings that are 1.5 cm on a side. Mating rings snap on to the open end of mating containers. Coupling rings, consisting of two plastic rings with the centers removed, are made by pressing the lids together back to back and sealing them together around the outer edge with plastic tape. These rings are used

TABLE 2. Summary of configurations in the modular, transportable habitat system.

Configuration	Size assembled		
	Small	Medium	Large
Mating cage with small-mesh screen	+	−	+
Mating cage with large-mesh screen	−	−	+
Storage cage	+	+	+
Emergence & indoor mating cage	−	+	+
Larval rearing cage (short)	+	+	+
Larval rearing cage (tall)	+	+	+
Larval rearing cage (extra tall)	−	+	+
Transport, field holding cage	+	+	+

to couple short or long tubes together to accommodate food plant cuttings of various heights. Both mating rings and coupling rings can be used as retaining rings when necessary.

Plant rings consist of one plastic lid with the center removed and one plastic lid with drilled or punched holes. The two lids are placed together back to back and sealed around the outer edge with plastic tape. They are used to join water containers and short or long tubes, with food plant cuttings placed through the holes into the water.

Netting is used to cover the tops of short or long tubes. Small-mesh netting, consisting of fine nylon hosiery material, is used to contain 1st- and 2nd-instar larvae. Large-mesh netting (0.3 cm openings) is used for later instar larvae. The large-mesh netting is also used on the top of containers which have been set up for emergence of adult moths.

Oviposition bags are brown paper bags used to hold female moths while they are depositing eggs. Plastic liners are plastic food bags used to line water containers. Paper liners consist of paper towelling used to line the inner surface of containers being used for the emergence of adult moths. Oviposition bags, and plastic and paper liners, are used once and discarded.

Modular System Configurations

Configurations of the modular, transportable habitat system are summarized in Table 2 and certain configurations are illustrated in Figs. 1 and 2.

Three types of mating cages are used in the modular system: small cages fitted with small-mesh mating rings; and large cages fitted with either small-mesh or large-mesh mating rings. No particular need was found for medium-sized mating cages, although this size could have been substituted for the large cages in the system, or could easily be added to the system if necessary. The main consideration in con-

structing and using the mating cages is to select a size to accommodate the adult moth and a screen size that prevents escape. Except for the method of access, and the fact that the large cages can be fitted with small-mesh rings, these mating cages are identical to the tubular mating cages described by Miller & Cooper (1976). Mating cages can be attached together in series, the closed end of one cage snapping into the mating ring of a preceding cage. In this way 6–8 cages can be transported in the field and unsnapped one at a time to be hung in suitable locations. Cages can be returned from the field by snapping them together as they are collected. The outdoor mating cages are known to work only for *H. cecropia, E. calleta, C. promethea,* and *A. polyphemus.* Other species have not been evaluated in the outdoor mating cages either because they are not indigenous to this area or because mating has been effected in the indoor mating cages.

Medium and large hatching cages are used to accommodate oviposition bags and food plant cuttings according to a method described earlier (Miller & Cooper, 1977). A large hatching cage is shown in Fig. 2 in the arrangement used to transfer newly-hatched larvae to food plants.

Medium and large indoor mating cages are used to store cocoons and pupae and to contain emerging moths prior to indoor mating or transfer to outdoor mating cages. The indoor mating cages are normally assembled using mating or water containers in an upright position with large-mesh netting held in place on top with retaining, coupling, or mating rings. Additional indoor mating cages can be assembled by replacing the mating or water containers with a short tube that has a plant ring snapped onto the bottom. In all indoor mating cage configurations paper towelling is used to line the inner surfaces. This permits emerging moths to climb up the sides onto the large-mesh netting to expand the wings and mate. In using these indoor mating cages the only handling of specimens involves the placement of cocoons or pupae in the cages for storage and the transfer of fertile females to oviposition bags after mating. All species that have been bred have readily mated in these cages. Because these indoor mating cages are used to minimize the effort required in maintaining indoor colonies, substantial numbers of cocoons and pupae are used at one time, and the moths that emerge and mate in the cages may have improperly expanded or damaged wings. However, the cages can be used to contain one or two cocoons or pupae when it is important to obtain undamaged moths.

The oviposition bags have worked satisfactorily for all species that we have reared, except *H. euryalis.* The females of this species do
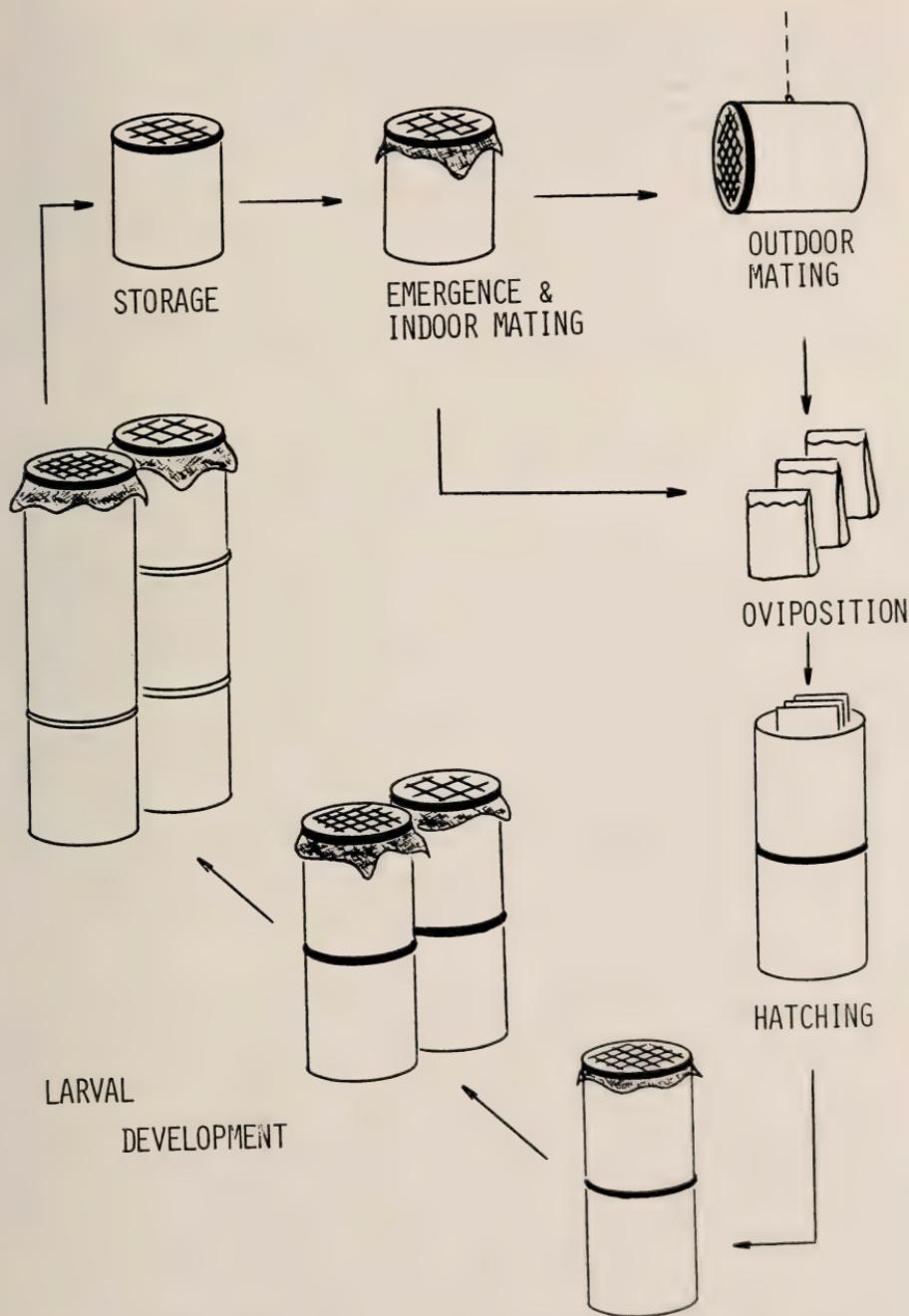
FIG. 3. A general rearing scheme using large components of the modular transportable habitat system.

not readily oviposit in the bags, and many individuals have remained in the bags for 5 or 6 days, depositing only a few eggs before dying.

Larval rearing cages are assembled using a water container, a plant ring, and some combination of short or long tubes with netting on top. Eight types of larval rearing cages (Table 2) are used to accommodate various sizes and numbers of larvae, and various sizes and types of food plant cuttings. The small larval rearing cages are used primarily for single larvae or small numbers of early instar individuals. The medium and large larval rearing cages are used as habitats for 3rd–5th instar larvae, where as many as 25 C. promethea or 12–15 H. cecropia or H. gloveri gloveri can be maintained.

Rearing Strategies

Since the components of the modular system can be arranged to accommodate most requirements, many rearing strategies are possible. Fig. 3 shows a general rearing scheme that is typical of the strategies used. Cocoons and pupae are stored in emergence and indoor mating cages. As the adults emerge they are either allowed to mate indoors or females are transferred to outdoor mating cages to attract wild males. Mated female moths, from either indoor or outdoor mating cages, are transferred to oviposition bags for collection of eggs. Shortly before the hatching of eggs, the oviposition bags are set up in a hatching cage with food plant cuttings. After larvae have hatched and transferred to food plant cuttings, the oviposition bags are removed. A fine-mesh net and retaining ring are added to the top of the hatching cage converting it to a larval rearing cage. Thereafter, larval rearing cages are assembled as required to provide habitats until cocoon formation occurs. The cocoons are then transferred to storage containers and held for adult emergence.

Modular System Evaluation

The effectiveness of the larval rearing cages was evaluated by comparing pupal body weights of C. promethea reared indoors in the modular system and outdoors in sleeve cages. The results (Table 3) showed that there was no significant difference in the pupal body weights produced in either system on each of two food plants. Data have not been collected on pupal body weights for other species. However, the various larval rearing cages have produced larvae that are satisfactory from the standpoint of general body size and percent survival for all species except H. gloveri gloveri, H. euryalis, and C. angulifera. Hyalophora gloveri gloveri can be maintained in the larval rearing cages, but all larvae are smaller than those reared outdoors in sleeve cages. Hyalophora euryalis larvae have not developed be-

TABLE 3. Comparative data for *Callosamia promethea* reared on two food plants in the modular system and in sleeve cages. Pupal weight in g.

Rearing system	Number replicates	Larvae per replicate	Mean percent pupating	Mean pupal[1] body weight
		Wild Cherry		
Modular	3	25	85.2	1.42
Sleeve	3	25	89.2	1.33
		Tuliptree		
Modular	3	25	80.0	1.22
Sleeve	3	25	77.2	1.43

[1] Body weights based on all pupae regardless of sex; means do not differ significantly at 0.05 level of probability.

yond the 4th instar when reared in the modular system. Approximately half of the groups of *C. angulifera* that have been reared in the modular system have succumbed to disease in the 4th or 5th instar.

All system components have been found to be of acceptable durability for both laboratory and field use. Some problems resulted from the rusting of water and mating containers, and from the failure of certain plastic parts. Although the inner surfaces of water and mating containers were sprayed with metal oxide primer and epoxy resin paint, rusting occurred around the top edges of these components when they were filled with water and the plant rings were in place. This problem was solved by the use of plastic liners. A few of the plastic components, especially the plant rings and the retaining rings, cracked after 3–4 years of use, but these were easily replaced.

ACKNOWLEDGMENT

LITERATURE CITED

COLLINS, M. M. & R. D. WEAST. 1961. Wild silkmoths of the United States. Collins Radio Co., Cedar Rapids, Iowa. 138 p.

CROTCH, W. J. B. 1956. A silkmoth rearer's handbook. The Amateur Entomologist's Society, London. 165 p.

DIRIG, R. 1975. Growing moths. New York State College of Agriculture and Life Sciences. 40 p.

MILLER, T. A. 1978. Oviposition behavior of colonized *Hyalophora gloveri gloveri* (Saturniidae). J. Lepid. Soc. 32(3): 233–234.

——— & W. J. COOPER. 1976. Portable outdoor cages for mating female giant silkworm moths (Saturniidae). J. Lepid. Soc. 30(2): 95–104.

——— & ———. 1977a. A method for handling eggs and 1st-instar larvae of *Callosamia promethea* (Saturniidae). J. Lepid. Soc. 31(2): 146–147.

———— & ————. 1977b. Oviposition behavior of colonized *Callosamia promethea*
    (Saturniidae). J. Lepid. Soc. 31(4): 282–283.
———— & ————. 1980. Oviposition behavior of colonized *Antheraea polyphemus* (Sa-
    turniidae). J. Lepid. Soc. 34: 204.
————, ———— & J. W. HIGHFILL. 1977. Determination of sex in four species of giant
    silkworm moth larvae (Saturniidae). J. Lepid. Soc. 31(2): 144–146.
———— & S. V. MACHOTKA. 1980. Sex-related morphological characters in larvae of
    Hyalophora gloveri gloveri and *Antheraea polyphemus* (Saturniidae). J. Lepid.
    Soc. 34: 69–73.
TASCHENBERG, E. F. & W. L. ROELOFS. 1970. Large-scale rearing of cecropia (Lepi-
    doptera: Saturniidae). Ann. Entomol. Soc. Amer. 63(1): 107–111.
VILLIARD, P. 1969. Moths and how to rear them. Funk and Wagnalls, New York.
    242 p.
WALDBAUER, G. P. & J. G. STERNBURG. 1973. Polymorphic determination of diapause
    by cecropia: genetic and geographic aspects. Biol. Bull. 145: 627–641.

TMOLUS AZIA IN JAMAICA: A NEW RECORD FOR THE
WEST INDIES (LYCAENIDAE)

Tmolus azia (Hewitson) occurs from southern Arizona and southern Texas south to
South America, and appears to have become recently established in Florida (T. C.
Emmel *in* Howe, 1975, The Butterflies of North America, Garden City; Lewis, 1973,
Butterflies of the World, London; H. K. Clench, pers. comm.)

On 12 February 1978 I collected a specimen of this species on the island of Jamaica,
about 11 km northwest of Mandeville, near the town of Kendall (Manchester Parish).
Subsequently, on 2 July 1978, I captured a second specimen on the grounds of the
Mount Forest Christian Youth Camp, 18 km south of Mandeville (elev. ca. 450 m).

This latter specimen is deposited in the Carnegie Museum of Natural History; I am
indebted to Harry K. Clench of that institution, who kindly identified this tiny hair-
streak and encouraged me to publish this note, and to Julian P. Donahue for his help
with the manuscript.

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AN ELEGANT HARNESS FOR TETHERING LARGE MOTHS

Like many an enthusiastic young lepidopterist, I used to tie soft strings around the "waists" of large female silkmoths and then set the captives out overnight to lure mates. Sometimes the results were positive, but only too often complications defeated me. If a moth decided to fly after dark, she might become badly entangled in her hopelessly twisted tether. On other occasions she would attempt to worm her way through the constricting belt, either succeeding in escaping or else becoming stuck half way through. In the latter case her abdomen was badly deformed and mating never occurred.

In recent years (slightly wiser and immeasurably older) I have realized that the "waist"—junction of thorax and abdomen—is not the optimum site for placing a belt, since that region remains permanently soft. A firm, strongly chitinized zone (after a moth has fully hardened) would be preferable. The best intersegmental cleft meeting that requirement lies between the meso- and metathorax. A tether should therefore pass between the fore and hind wings, and between the second and third pairs of legs.

In dealing with those smaller anatomical parts, I found that ordinary string was too coarse. Twelve-pound test nylon casting line looked ideal, but I was afraid it would cut into the moth's thorax when she began her evening efforts to fly. To avoid twisting of the line, I decided to use a swivel, just as fishermen do for the same reason. It remained to find a way to fit the moth comfortably into a harness of this material.

At a hobby shop I found short lengths (ca. 30 cm) of thin brass tubing, imported from Belgium, and used by model airplane builders. Outside diameter was 2.25 mm, bore about 1.75 mm. These were the only moderately expensive items in my kit. Even so, I cut a single tube into 4 cm sections to give me pieces for seven harnesses. Probably one can obtain plastic tubing of similar size that is cheaper. The rest of my outlay included a small bag of beads, such as are used to adorn Indian moccasins, sewing needles, a package of spring clothespins, a box of small flat-headed nails, and a few old rusty paperclips.

To prepare a harness, I had first to thread a needle with the casting line. That was the hardest part, because the needle must be small enough to pass through both the brass tube and the beads, yet with a large enough eye to accommodate the line. The procedure then was as follows. Thread a bead on the line, pass the needle through the tube, thread another bead on the line. Now reverse the process. Pass the needle back through the second bead (making sure not to pull the loop through, thus undoing all this work!), back through the tube, and back through the first bead. The harness was now ready, as shown in Fig. 1.

Why the beads and the tube? Perhaps the beads weren't really necessary, but they made the harness flexible by providing moveable joints. I incorporated them mainly to avoid friction against the cut edge of the tubing. The beads' smooth surfaces protected the line against damage when a moth became active.

The tubing was also a protective piece. Whatever part of the harness might snarl when a moth attempted to fly must be beyond the extent of her wing tips. With the tube attached to a swivel at that point, the moth could gyrate indefinitely without becoming fouled. A length of four or five cm gives adequate clearance.

The only remaining need was to attach the swiveled tether to some fixed point. If I had simply passed a string through the other end of the swivel, I would still have had the problem of tying the string to something else. As a matter of fact I did have a number of pre-chosen fixed points that I wanted to use repeatedly. These were inverted peach baskets, hung strategically from various trees and outbuildings on my farm in Eldora, Cape May County, New Jersey. A wooden spring clothespin was suspended from the center of each. One side of the clothespin was pierced by a small flat-headed nail. Before setting out a tethered moth, I passed a paper clip through the far end of her swivel. When the other end of the paper clip became engaged by the nail in the clothespin, it could not possibly be pulled out by a struggling moth.

After a bit of practice I was able to prepare a harness in only a minute or two and to apply it to a moth in an equally brief time. Moths appear to adapt to this form of
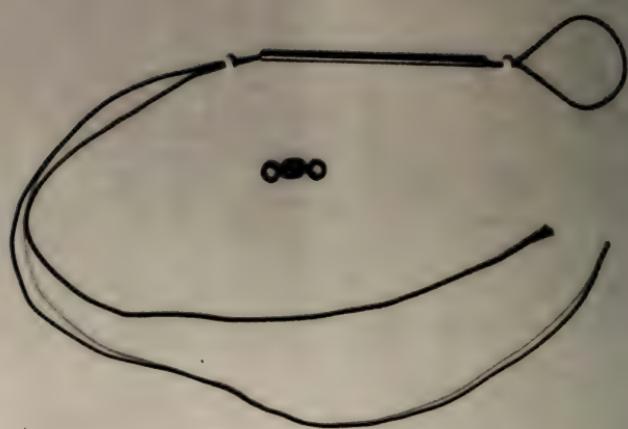
FIGS. 1, 2.

restraint without undue resistance. I have used it successfully with a long series of *Citheronia regalis, C. sepulcralis* and *Eacles imperialis.* The photograph (Fig. 2) depicts one of those matings.

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NOTES ON *GRACILLARIA ELONGELLA* (GRACILLARIIDAE) WITH A DESCRIPTION OF THE LARVAL MOUTHPARTS

Since the hostplant records for *Gracillaria* (=*Gracilaria*) help form the basis for the taxonomy of the genus (Forbes, 1923, Cornell Univ. Agric. Expt. Sta., Mem. 68: 1–729) these records should be completely and precisely catalogued. Therefore, it is noteworthy that *Gracillaria elongella* (Linn.) has been reared from yellow birch, *Betula alleghleniensis* (=*Betula lutea*) at the Hubbard Brook Experimental forest in Grafton Co., New Hampshire, because Forbes (loc. cit.) previously recorded alder as its only host.

The adult was needed for positive species identification so only the cast skin of the larva was used to draw the figures, instead of material preserved in alcohol. Forbes (1910, Ann. Entomol. Soc. Amer. 3: 94–125) stated that this method will produce satisfactory material for descriptions with the obvious advantage of associating a known adult with a larval skin. Four individuals were examined. All drawings were done under a compound microscope.

The hypopharyngeal complex is shown in Fig. 1 with terminology of Godfrey (1972, USDA Tech. Bull. No. 1450, 256 p.) and DeGryse (1915, Proc. Entomol. Soc. Wash. 17: 173–178). A pair of stipular setae are present. The proximomedial area bears a single row of ten stout blades flanked by smaller spines on either side. The distal spines cross the medial transverse cleft into the proximolateral region. The spinneret is blunt. DeGryse (loc. cit.) pictured an unidentified *Gracillaria* larva (from alder) which had a blunt spinneret and blades also. However, in contrast to *Gracillaria elongella,* that individual had the first three blades much reduced, not subequal (Fig. 1). Whether this represents intraspecific variation or another species is not known. MacKay's studies (1972 Can. Entomol. Mem. No. 88, 83 p.) on *Gracillaria syringella* showed a "broad spinneret, with silk pore dorsal at the apex."

The mandible (Fig. 2) has four sissorial teeth. The inner ridge bears an associated tooth also. A pair of lateral mandibular setae are present. The mandibles can provide useful specific characters in some cases (Forbes, 1910, loc. cit.), but they can change throughout the life of the larva (Embree, 1958, Can. Entomol. 40: 166–174; Fracker, 1915, Ill. Biol. Monogr. 2(1): 1–166). Dimmock (1880, Psyche 3: 99–103) stated that the mandible of *Gracillaria syringella* retained the same general form throughout larval life in contrast to the variability known in other species.

The chaetotaxy of the adfrontal area is shown in Fig. 3 with terminology after Hinton (1946, Trans. Roy. Entomol. Soc. Lond. 97: 1–37) who mentioned the position of the adfrontal (AF) setae as a useful specific character. Most *Gracillaria* have AF1 and AF2 well-separated (Forbes, 1910, loc. cit.), so *Gracillaria elongella* may be unusual in this respect, since it has the above two setae fairly close together. Unfortunately, the frontal setae group was damaged. The clypeal setae are subequal and arranged as shown.

The labrum is shown in Fig. 3 with nomenclature after Forbes (1923, loc. cit.). The chaetotaxy is shown on the left and the distribution of microspines on the right. L2 is slightly larger than L1 or L3. The medial group appears to have all setae subequal.

No information is available on the chaetotaxy of the thorax and abdomen although their size is definitely not minute, as stated by Fracker (1915, loc. cit.). MacKay (1972
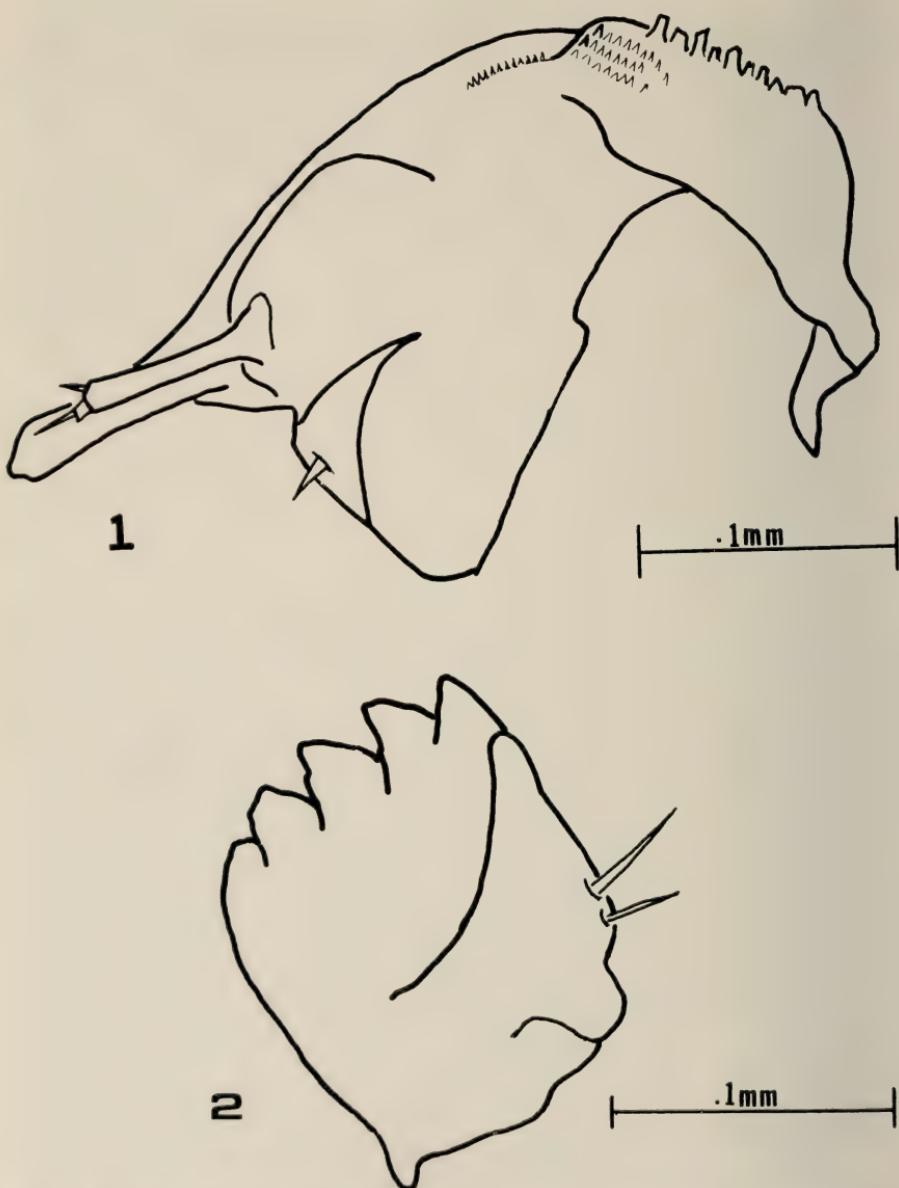
FIGS. 1–2. Larval mouthparts of *G. elongella*. 1, hypopharyngeal complex, lateral view; 2, mandible, ventral view.

Can. Entomol. Mem. No. 88, 83 p.) gives probable group characteristics based on *Gracillaria syringella*.

The addition of yellow birch as a host is not surprising. Stainton (1864, *Natural History of the Tineina*, London, 8: 72–75) cites Buxton as "noticing the larva on birch" in Europe, although all North American forms had been bred from alder, according to Forbes (1923, loc. cit.). Stainton (loc. cit.) described and pictured the superficial char-
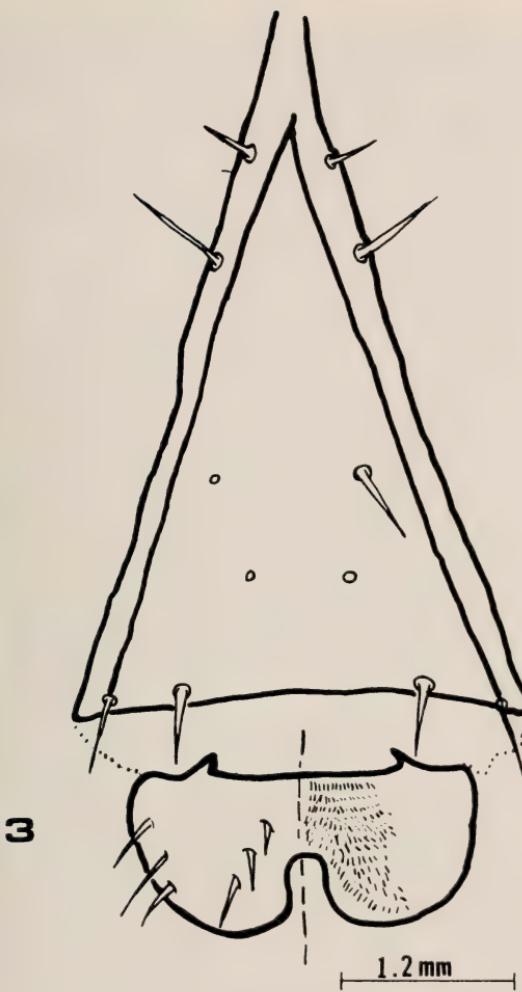
FIG. 3. Adfrontal area and labrum of *G. elongella*.

The larva rolls a leaf in a cone-shaped fold. The pupa is usually spun near the leaf edge in an oval, transparent cocoon, and is protruded at emergence. The caterpillar may be collected in July and the moths emerge in August of the same year.

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OVIPOSITION BY *HELICONIUS HECALE* (NYMPHALIDAE) ON A GRASS INFLORESCENCE IN COSTA RICA

Oviposition by *Heliconius* butterflies (Nymphalidae: Heliconiinae) involves the use of innate or learned searching images (Gilbert, 1975, *In* Coevolution of Animals and Plants, pp. 210–240, L. E. Gilbert & P. H. Raven, eds., Austin: Univ. Texas Press, 246 p.; Benson et al., 1975, Evolution 29: 659–680). Such search images, which function to insure that *Heliconius* place eggs on the correct species and structures of Passifloraceae, their larval host plants (Ehrlich & Raven, 1965, Evolution 18: 586–608), represent sophisticated behavioral traits. *Heliconius* have been seen to ignore an inconspicuous host plant to inspect another plant resembling a *Passiflora* structure such as a tendril (Benson et al., 1975, loc. cit.). However, it is not known whether *Heliconius* will actually place eggs on such incorrect hosts. Therefore observations made in the wild of any species of *Heliconius* placing eggs on inappropriate plants adjacent to a host plant are important. This note describes an observation of *Heliconius hecale* (Fabricius) placing an egg on a grass inflorescence near a small *Passiflora vitifolia* H.B.K. vine. This is the first published record of such behavior to my knowledge.

On 3 August 1978, a fresh female *H. hecale* spent several minutes inspecting a small (immature) vine of *P. vitifolia* tangled in grass (unidentified) at the edge of a mixed cocoa (*Theobroma cacao* L.) and rubber (*Hevea brasiliensis* Muell. Arg.) plantation at "Finca El Uno" near La Virgen (220 m elev.), Sarapiqui, Heredia Province, Costa Rica. A single egg was placed on the tip of a long uncoiled tendril at 1015 h, and a few minutes later, another egg was placed on a grass inflorescence a few centimeters from the *P. vitifolia* vine (Fig. 1). The butterfly then flew away. A 20 min inspection of the vine and surrounding grass failed to turn up any additional eggs of *H. hecale* or other *Heliconius* (see also Young, 1978, Entomol. News 89: 81–89 for species using *P. vitifolia* at this locality). This vine was about 0.75 m long and, with the exception of the single uncoiled tendril, it was tangled in the grass, and lying tucked away below the canopy of the grass. Other tendrils were tightly coiled around grass stems and leaves and they were hidden from view. No other vines of *P. vitifolia* were within 30–40 m of this one. This vine had five unfolded leaves and no *Heliconius* larvae were present.

While it is known that heliconiines such as *Dryas iulia* (Fabricius) and *Agraulis vanillae* (L.) place eggs on adjacent plants, dead leaves, and other objects near their passifloraceous host plants (Benson et al., loc. cit.), this behavior is less known for *Heliconius*. Coupled with a tendency for larvae to wander in search of the correct host plant, such behavior has been speculated to be adaptive in reducing losses of eggs to predators (Benson et al., 1975, loc. cit.). Most species of *Heliconius* exhibit precise oviposition on the correct host plants (e.g., Alexander, 1961, Zoologica 46: 1–24; Gilbert, 1975, loc. cit.; Benson et al., 1975, loc. cit.; Young, 1973, Wasmann J. Biol. 31: 337–350; 1975, Pan-Pacif. Entomol. 51: 76–85; 1976, Pan-Pacific Entomol. 52: 291–303; Smiley, 1978, Science 201: 745–747). Although the hypothesis that heliconiines (including *Heliconius*) lay eggs on plants and objects adjacent to host plants to reduce losses of eggs from predators, cannot be ruled out, a recent study (Smiley, 1978, loc. cit.) suggests that ecological factors determine oviposition preciseness in *Heliconius*. In Costa Rica *H. hecale* exhibits careful oviposition of eggs singly on the tips of both coiled and uncoiled tendrils of *P. vitifolia* (Young, 1975, loc. cit.; 1978, loc. cit.) and owing to this species' close affinities to *H. erato*, it is most likely monophagous locally (Smiley, 1978, loc. cit.). Given these ecological properties, the observed instance of oviposition on a grass inflorescence probably resulted from confusion in the searching image: the grass inflorescence probably was confused with the elongate uncoiled tendril of *P. vitifolia* only a few cm away. However, the presence of only one free-hanging tendril induced the butterfly to later oviposit on the grass inflorescence. Sometimes butterfly oviposition on incorrect or inappropriate plants is due to the rarity of the favored or correct host plant (Chew, 1977, Evolution 31: 568–579).

This observation and the general conceptual framework on *Heliconius* oviposition strategies and host plant exploitation (Gilbert, 1975, loc. cit.; Benson et al., 1975, loc. cit.) suggest that occasional instances of incorrect oviposition by *Heliconius* are in-

FIG. 1. Above: The position of the grass inflorescence used for oviposition by *H. hecale* relative to the position of the *P. vitifolia* vine (trilobed leaf in center) is shown. Arrow indicates location of the egg. Below: the position of the egg on the grass inflorescence, indicated by the arrow.

duced by ecological factors such as scarcity of the host plant, host plant patch size, scarcity of host plant structures suitable for oviposition, and resemblances of surrounding plants to the host plant. In the present instance, *H. hecale* might have been induced to oviposit on the grass inflorescence by these properties of the *P. vitifolia* "island."

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JAMES MASON HUTCHINGS (1824–1902): AN EARLY BUTTERFLY COLLECTOR IN CALIFORNIA

J. M. Hutchings is known to have supplied specimens of *Parnassius phoebis behrii* W. H. Edwards to Henry Edwards (cf. Edwards, 1878; Proc. Cal. Acad. Sci. 11–14). F. M. Brown (1975, Trans. Amer. Entomol. Soc. 101: 1–31) credited him with taking the type specimen of *P. behrii* near the summit of Mount Lyell, and as possibly being the collector of the type specimen of *Parnassius clodius baldur* W. H. Edwards. Hutchings undoubtedly collected Lepidoptera for Henry Edwards, and possibly for others. Biographical data on him will be important, especially if additional material originating from him should be discovered in other collections. He did not, however, collect the type specimen of *Parnassius behrii* (cf. accompanying note, Masters, J. Lep. Soc. 34: 47).

Hutchings was born in England in 1824. He came to the United States as a youth and to California in 1849 after news of the gold discovery reached him in New Orleans. He worked in the mines for a few years before turning to writing and publishing. From 1856 to 1861, he published Hutchings' California Magazine, which was widely acclaimed as one of the best illustrated magazines of its day. In 1855, accompanied by a daguerreian cameraman, he led the first tourist party into Yosemite Valley. His account of this trip appeared in his magazine and was widely reprinted; it is generally credited with stimulating most of the early interest in Yosemite.

Hutchings sold his magazine in 1861 and bought the "Upper Hotel" in Yosemite, which he renamed "Hutchings House." This he operated as a guest house. He was a permanent resident of Yosemite Valley from this time until his death in 1902. One of his first employees in Yosemite was John Muir, who worked for him as a carpenter. He and Muir soon parted company as a result of differences in philosophy involving Yosemite Valley. Hutchings wanted to see the valley commercially developed, while Muir wanted it preserved as a wilderness. [It is unlikely that either of them would be happy with Yosemite today. Although it is preserved in the National Park System, it is the most populated, commercialized, and highly developed part of that system.]

During Hutchings' Yosemite years he continued to explore California's unusual places, and he produced a series of privately published books concerning his travels (e.g., 1877, A Guide to Yosemite; 1886, The Heart of the Sierras; 1894, Yosemite Valley and the Big Trees). In none of these writings did Hutchings mention butterflies. However, he did publish a number of items on other phases of California natural history, including flowers, animals, horned toads and various articles on birds. More complete data on Hutchings is provided by Olmsted (1962, Scenes of Wonder & Curiosity, Howell-North, Berkeley) and by Farquhar (1965, History of the Sierra Nevada, U. Calif. Press, Berkeley).

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SEX-RELATED MORPHOLOGICAL CHARACTERS IN LARVAE OF
HYALOPHORA GLOVERI GLOVERI AND
ANTHERAEA POLYPHEMUS (SATURNIIDAE)

Information on sex-related morphological characters that occur in giant silkworm moth larvae has a number of useful applications, including: determination of sex in individual larvae, maintenance of proper sex ratios in breeding stock, rearing of one particular sex for special research purposes, and determination of sex ratios in experimental groups of individuals without having to rear them to pupation or adult emergence. Sex-related morphological characters have been reported for a number of lepidopterous larvae (Stehr & Cook, 1968, Bull. U.S. Nat. Mus. 276: 46–47; Hinks & Byers, 1973, Can. J. Zool. 51: 1235–1241; Kean & Platt, 1973, J. Lepid. Soc. 27: 122–129; Miller et al., 1977, J. Lepid. Soc. 31: 144–146). These characters vary somewhat in form, but they appear to represent either the genital histoblasts, visible externally through the integument; or pits or modifications of the integument associated with the genital histoblasts. In female larvae the genital histoblasts, or modifications of the integument, are found as paired structures on the venter of the 8th and 9th abdominal segments (S8 and S9). In male larvae the genital histoblast, or the modified integument, is found as a single structure on the venter of S9. Examination of 4th- and 5th-instar larvae of four giant silkworm moth species (Miller et al., 1977) demonstrated the occurrence of these characters in male larvae of *Antheraea polyphemus* (Cramer); and in female larvae of *Eupackardia calleta* (Westwood), *Hyalophora cecropia* (Linnaeus), and *Callosamia promethea* (Drury). This paper reports the occurrence of such characters in another giant silkworm moth species, *Hyalophora gloveri gloveri* (Strecker), and provides additional observations on characters previously reported by Miller et al. (1977) for *A. polyphemus*.

The *H. gloveri gloveri* larvae used in this study were from a small breeding-stock colony maintained in sleeve cages on wild black cherry (*Prunus serotina*) in Frederick Co., Maryland. Newly-hatched, 1st-instar larvae were set up in a separate sleeve cage on wild black cherry. They were removed from the sleeves as early 5th-instar individuals and categorized as male or female on the basis of the morphological characters discussed earlier. The larvae were then segregated according to sex into two sleeve cages and reared to pupation to confirm the sex of each individual. A small number of other early 5th-instar individuals from the same original sleeve cage were killed in neutral buffered formalin. These larvae were used, as freshly-killed individuals, to photographically record the appearance of the external morphological characters; and later for histological sectioning and examination for internal histoblasts. In the larvae for histological sectioning, the appropriate abdominal segments (S8 for females; S9 for males) were removed with a scalpel. The fixed abdominal segments were embedded in paraffin, sectioned at 6 μm, and stained with hematoxylin and eosin. Seventeen living 5th-instar larvae of *H. gloveri gloveri* were examined for external morphological characters. Seven individuals possessed fairly distinct, white, subsurface spheres between the ventral and subventral setae on S8 and S9 (Fig. 1) and were categorized as females; 10 individuals possessed a single, dark pit on the venter of S9 (Fig. 2) and were categorized as males. These larvae, after being segregated and reared to pupation, produced 7 female pupae and 10 male pupae corresponding to, and confirming, the sex determinations made in the larval stage. Examination of transverse sections prepared from female larvae of *H. gloveri gloveri* did not reveal any structures that could be related to the white, subsurface spheres that had been observed in living specimens. These negative findings are presently without explanation. It is possible that the spheres observed in living larvae were lost in sectioning, particularly if they did not have a firm attachment to the integument. Also, it is possible that the structures that we observed externally were missed in the sectioning process, since we could not prepare thin sections for the entire larval abdominal tissue. Transverse sections from male *H. gloveri gloveri* larvae revealed the presence of an internal structure (Fig. 3) associated with the dark pit observed in living larvae. This structure is similar in form
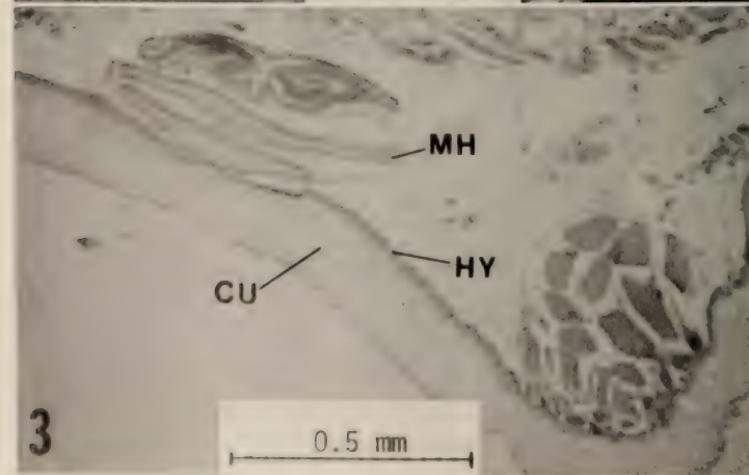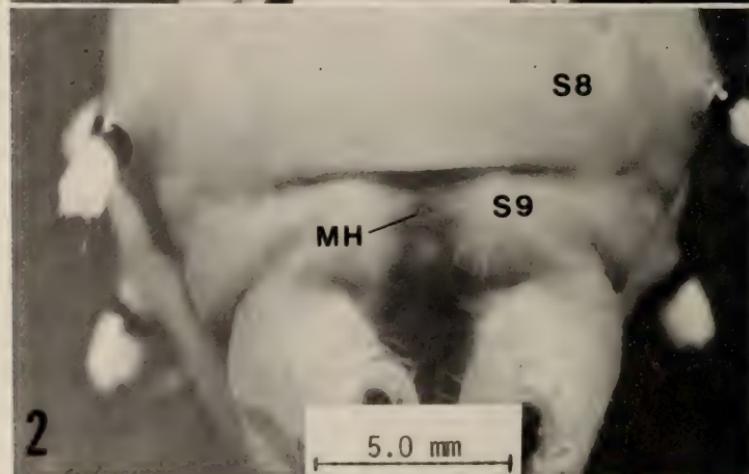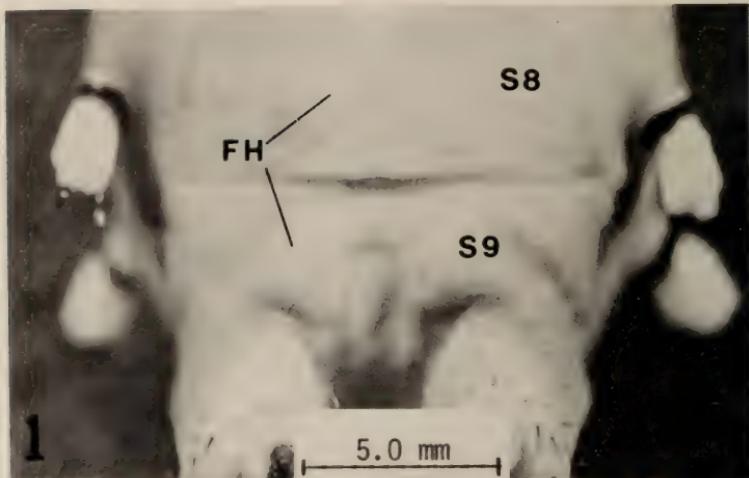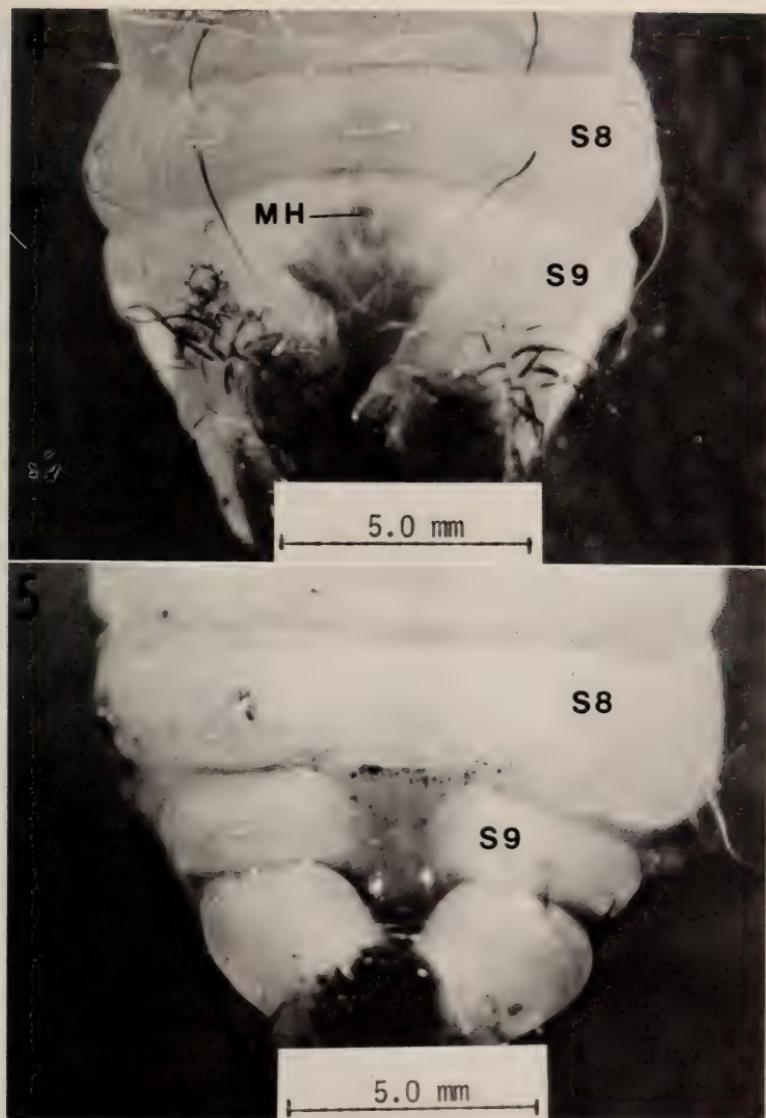
FIGS. 4–5. Ventral views of 5th-instar *A. polyphemus* larvae. 4, male showing location of black pit (MH) associated with histoblast on S9. 5, female showing absence of any external structures associated with histoblasts on S8 and S9, and absence of black pit on S9.

←

FIGS. 1–3. Sex-related morphological characters in 5th-instar larvae of *H. gloveri gloveri*. 1, ventral view of female showing white, subsurface spheres (FH) associated with histoblasts on S8 and S9. 2, ventral view of male showing dark pit (MH) associated with histoblast on S9. 3, transverse section of S9 of male showing single histoblast associated with dark pit observed externally in living larvae. CU, cuticle; FH, female histoblast; HY, hypodermis; MH, male histoblast.
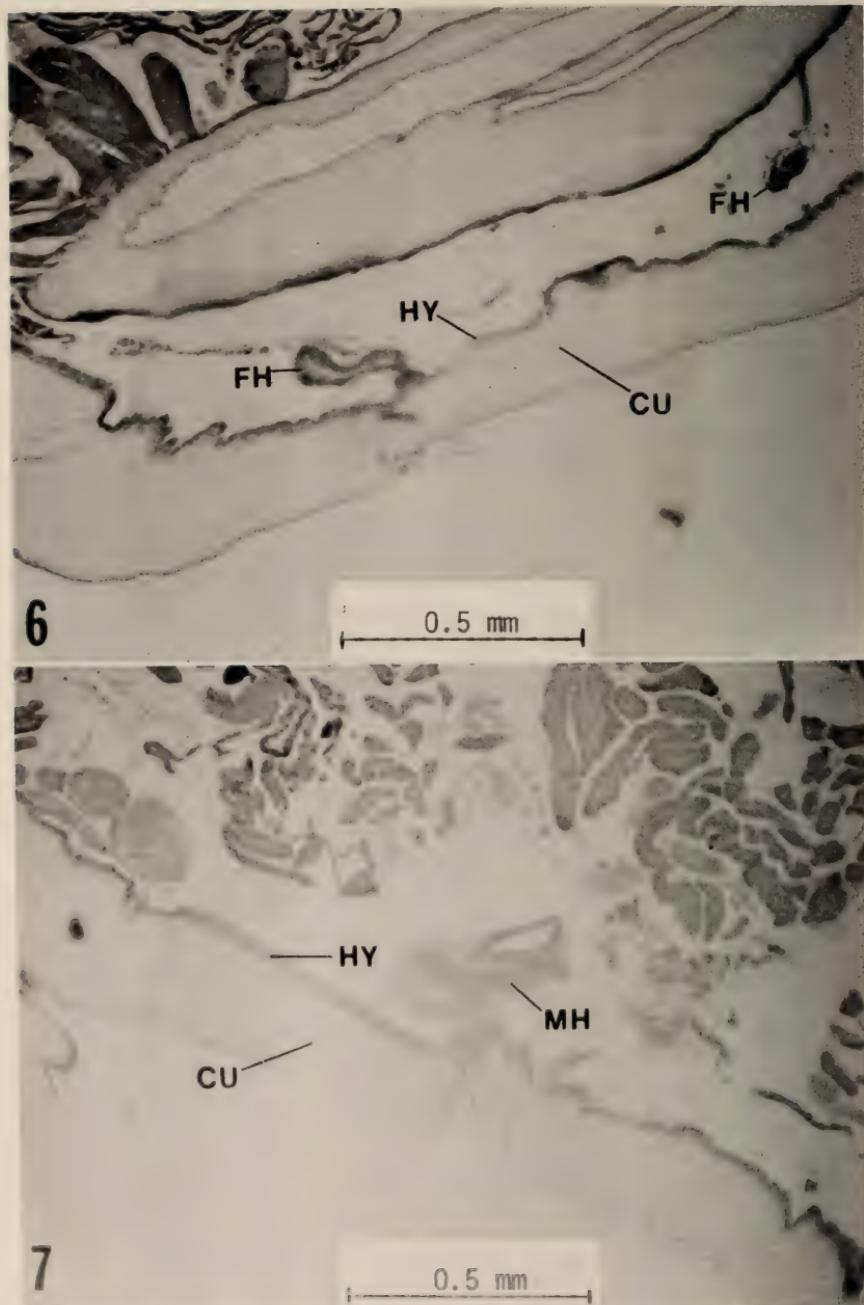
Figs. 6–7. Transverse sections of venter of S8 and S9 of 5th-instar *A. polyphemus* larvae. 6, female showing paired histoblasts in S8. 7, male showing single histoblast associated with black pit on S9. CU, cuticle; FH, female histoblast; MH, male histoblast; HY, hypodermis.

to the male histoblast (Herold's Organ) described by Hinks & Byers (1973) for noctuid larvae and probably represents the male genital histoblast in *H. gloveri gloveri.*

The *A. polyphemus* larvae used in this study were from a colony maintained in sleeve cages on various maples (*Acer* spp.) in Frederick County, Maryland. During routine maintenance of the colony, we have cursorily examined 4th- and 5th-instar larvae for the presence of external sex-related characters. After several hundred such examinations, we have observed only the male character, in the form of a black pit on the venter of S9, as described earlier by Miller et al. (1977). To improve our ability to reliably determine sex in larvae of this species, we made more detailed examination of a series of individuals. The objective was to locate and describe any external female characters that correspond in form and location to those found in females of other species discussed heretofore. If characters thought to represent female histoblasts were observed, we planned to rear larvae to pupation to verify sex. Larvae were removed from the sleeves as early 5th-instar individuals and examined with the unaided eye for the presence or absence of the black pit characteristic of the male; those without a black pit were examined in greater detail for the presence of female characters using a dissecting microscope (60×). A few 5th-instar larvae from the colony were killed in neutral buffered formalin and used, as freshly-killed individuals, to record photographically the external appearance of S8 and S9; and later for histological sectioning and examination for histoblasts. Histological sectioning was accomplished in the same manner as discussed earlier for *H. gloveri gloveri.* We examined forty-nine 5th-instar larvae of *A. polyphemus.* Nineteen of these had a black pit on the venter of S9 (Fig. 4). In the other 30 individuals we could find no characters that appeared to represent either male or female histoblasts, or modifications of the associated integument, on S8 or S9 (Fig. 5). Although these conditions were described earlier by Miller et al. (1977), they were not illustrated; therefore, we have included them here as figures. Since no female characters were observed, we did not rear any of these 49 individuals to pupation to confirm sex. The information presented by Miller et al. (1977) adequately demonstrated the sex-related nature of the black pit (i.e., pit present = male; pit absent = female) and additional confirmatory data based on our observations was not necessary. In the female *A. polyphemus* larvae, transverse histological sections revealed the presence of paired, pyriform histoblasts (Fig. 6) arising from the ventral hypodermis in the areas between the ventral and subventral setae of S8. There were no apparent modifications of the associated integument, an observation that was also made during examination of living larvae. Transverse sections from male *A. polyphemus* larvae revealed the presence of an internal structure (Fig. 7) associated with the black pit observed in living larvae. This structure, which is elongate and appears to have a firm attachment to the hypodermis, appears to represent the male genital histoblast in *A. polyphemus.* It is similar to the male histoblast (Herold's Organ) described for noctuid larvae by Hinks & Byers (1973).

We have concluded from these observations that the presence of sex-related morphological characters in *H. gloveri gloveri* is confirmed; and that the characters can be reliably used to sex larvae of this species. Although we found both male and female histoblasts in larvae of *A. polyphemus,* those of the female are small and not visible externally; and the associated integument is not modified. Therefore, we have concluded that living larvae of *A. polyphemus* can be sexed only on the basis of the presence or absence of the male character.

THOMAS A. MILLER, *U.S. Army Medical Bioengineering Research* & *Development Laboratory and* SAMUEL V. MACHOTKA, *U.S. Army Medical Research Institute of Infectious Diseases, Fort Detrick, Maryland 27101.* (The opinions contained herein are those of the authors and should not be construed as official or reflecting the views of the Department of the Army.)

A POSTSCRIPT TO THE AUTHORSHIP OF *HESPERIA MYSTIC*

Sometime ago I published an article alleging that W. H. Edwards was the author of *Hesperia mystic* in 1863, and that Scudder's use of the name should be dated from 1864 (F. M. Brown, 1966. J. Lepid. Soc. 20: 239–242). Since then I have received from my good friend, Mr. A. S. Pinckus, a copy of the rare Scudder preprint of the article in which he published the name *mystic*. Some years earlier the librarian of the Essex Institute, Salem, Massachusetts, and I searched the archives of the Institute for any evidence that such a preprint had been published through official channels. We could find none, although the records of both the secretary and treasurer of the Institute (for the years involved) were open to us. The only explanation for the Scudder preprint is that he ordered it directly from the printer, bypassing the Institute. Its existence requires that the authorship of *mystic* be re-examined.

In 1863, few, if any but the largest printers, could afford to hold in forms more than a signature or two at a time due to the shortage of type. Generally, a signature was set, locked, and proofed in page. When the proofs had been approved, the signature was run in requisite numbers and the ordered preprints were printed. Preprints usually were done in a rearranged form, but the original pagination was retained. When all of the signatures of a book had been run, they were collected, sewed, and then bound.

Two dates are important for articles in journals printed in this fashion: The first is the date upon which the preprint was released by the author. This date can rarely be ascertained. If a preprint is dated, it can be assumed that the author distributed it to correspondents within a month of the preprint date. However, there are exceptions. For example, the March–April, 1871, parts of the Transactions of the American Entomological Society were not finished until August, or very early September of that year. The ICZN has given unofficial approval for using preprint dates for reasons of priority (1977, ICZN, Edition 3, Internat. Trust for Zoological Nomenclature, London).

The second important date is the date of issue of the regular part of a journal or a book. This is often not easily discovered for 19th-century publications. Considerable research is needed to verify masthead or title page dates. Often one can trace dates of receipt at institutional libraries noted in accession lists. When only the year-date is known, the publication is assumed to have been made on 31 December of that year. Similarly, when a month-date is known, publication is assigned to the last day of that month. This holds for preprints as well as for journal parts or books.

Supporting evidence is necessary before using dates other than these for publication. Sometimes such evidence is internal and direct: for example, masthead dates, or statements by the editor about the precise date of issue are satisfactory. Indirect evidence of various kinds may come from outside the publication itself, for example, reviews or letters about the publication, or official records of the institution involved.

Let me turn to the evidence in the case of *mystic* Edwards (W. H. Edwards, 1863, Proc. Entomol. Soc. Phila. 2: 14–22), vs. *mystic* Scudder (S. H. Scudder, 1863, Proc. Essex Inst., Salem, Mass., 3: 161–179). The former was published in March and April, 1863, whereas, the latter was published as a whole volume; the preprint was dated April, 1863. The important information for establishing priority is given below:

Evidence	*mystic* Edwards	*mystic* Scudder
1. Credit by authors	to Scudder	to Edwards
2. Preprint date	March 1863	April 1863
3. Date of issue of part or volume	29 July 1863	Between 28 Dec. 1863 and 26 April 1864

The evidence throughout is that Edwards published the name *mystic* before Scudder did. However, the preprint data must be examined more closely. The paper in which Edwards published *mystic* straddled the 1st and 2nd signatures. Although *mystic* was published in signature 1, dated March 1863, the rest of the article appeared in signature 2, dated April 1863. Thus both Edwards' and Scudder's preprints must be dated 30

April, 1863. This leaves us with only the journal part and book release dates as the basis for settling the dispute. Edwards wins that by more than five months. It does not matter that Scudder had used *mystic* orally (giving credit to Edwards) at a meeting on 10 March 1862. The valid name is *mystic* Edwards, 1863, as previously concluded.

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THE OCCURRENCE OF *CHLOROCLYSTIS RECTANGULATA* (GEOMETRIDAE) IN NEW BRUNSWICK

On 14 July 1978, while operating a UV light at Sussex, Kings Co., New Brunswick, I took a worn male moth resembling one of the many *Eupithecia* species, which, upon closer inspection, appeared to be the introduced European species *Chloroclystis rectangulata* (L.). This was later confirmed by genitalic dissection.

This record constitutes the first known occurrence of this species in North America outside the province of Nova Scotia, and a new record for the province of New Brunswick. *C. rectangulata* was first collected in 1970 by D. C. Ferguson and B. Wright from localities in Hants and Victoria counties, Nova Scotia (Ferguson, 1972, J. Lepid. Soc. 26: 220–221) and has since become quite common in some areas of the province, especially around Halifax. The specimen is in the author's collection.

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BOOK REVIEWS

LES ATTACIDAE AMERICAINS . . . THE ATTACIDAE OF AMERICA (=SATURNIIDAE) ATTACINAE by Claude Lemaire. 1978. Édition C. Lemaire, 42 boulevard Victor Hugo, F-92200 Neuilly-sur-Seine, France. 238 pp., 49 pls. Price: US $60.00.

This is a revision of the New World moths of the subfamily Attacinae (=Saturniinae). The plates of imagines are black & white photographs but are high quality, clear, and on a 1:1 scale. The text is in French. Under each taxon there is a substantial English summary; thus the bilingual title. Figures include distribution maps of several taxa and line drawings of male *and female* genitalia (which the author calls genital armature) of each species, except for a few species where the females remain unknown. These line drawings are accurate and useful; the aedeagus is figured from the lateral and dorsal views. This is the first time that female genitalia are figured for some of our commonest species such as *Hyalophora cecropia* and *Actias luna*. Drawings of legs, antennae, and wing venation are provided for some species. In this book we find numerous species figured for the first time since their original descriptions. Figures of some females are the first ever published.

Regarding systematics the work is thorough. As usual, Lemaire follows the International Code of Zoological Nomenclature rigidly, correcting errors of earlier authors. Each taxon has lists of synonymies, type information and localities. In his lists of synonymies Lemaire even includes quadrinomials of Bouvier although the Code does

not require this. The text contains 83 original lectotype designations, although some of these refer to published figures of lost specimens. There are introductory chapters on geographical zones, the typological concept, higher taxonomy, morphology and speciation. Under each genus is a key to the species. Two new species are described in this work, both in the genus *Copaxa*.

As a part of this review I must also point out errors although these are fully overshadowed by the good aspects. Misspellings include *Dryocompa* for *Dryocampa* on p. 8, Schwandner for Gschwandner on p. 13, Saturnioidaea for Saturnioidea on p. 23. Certain Spanish and Portuguese locality names are missing accents where appropriate e.g. Nuevo León). The wording of some of the English sentences is awkward although this is not the fault of the French author, but of his British "friend" who worked on these parts. English errors on p. 124 are tamarak for tamarack, and Douglas pine for Douglas fir. An inexcusable error is misspelling Colombia as Columbia.

In my opinion, the badly needed revision of the extensive genus *Rothschildia* is a major feature of this book. The key to the species is usable but some couplets refer to genitalic structures. I question Lemaire's subspecies concept in a couple instances in this genus, such as two subspecies of *R. orizaba* occurring (sympatrically except for altitude) in the Cauca Valley of western Colombia. Amateur lepidopterists will be surprised to learn of Lemaire's conclusions that *forbesi* is a subspecies of *R. lebeau* and that the true *R. jorulla* does not occur in the United States; *R. cincta* is the species in Arizona and neither *R. jorulla* nor *R. cincta* occur in Texas, this latter conclusion agreeing with my own field observations in southern Texas. Lemaire can aptly deal with the saturniid fauna of the United States because he is intimately familiar with their neotropical congeners.

Under *Samia* there are good morphological comparisons with Asiatic species. No mention is made either to support or refute published reports that *S. cynthia* was introduced and established in Cuba and Montevideo, Uruguay. Faith is still being put in the report of *S. cynthia* in Savannah, Georgia but I have searched for this species in that city and conclude that this record strongly needs verification before being perpetuated further in the literature.

In *Hyalophora* Lemaire considers *gloveri, nokomis,* and *columbia* to be conspecific. He points out that *columbia* is the nominate subspecies, since it is the oldest proposed name. In *Antheraea* and *Actias* this revision reveals a lot about the Mexican relatives of our North American species. Two specimens in the Texas A&M University Entomology Department Collection give significant range extensions to add to Lemaire's records: *Antheraea polyphemus mexicana* from Sierra del Carmen, Coahuila, and *A. p. oculea* from 25 km W of Linares, Nuevo León.

Copaxa is a large widespread genus which also needed revision. *Sagana* and *Saturnoides* are here synonymized under *Copaxa* instead of being considered subgenera or full genera. To the given records of *C. muellerana* I can add Jocotepec, Jalisco from a specimen in my collection. Under *Saturnia* Lemaire does use subgenera: *Saturnia, Eudia,* and *Calosaturnia*. A lot of attention is given to this matter including larval characters and genitalia. I see little reason not to consider the Eurasian *Eudia* congeneric with the three Californian species, except that Europeans would not accept *Calosaturnia* (a name older than *Eudia*) as the generic name for their species such as *pavonia*.

This book should be in every museum and university library. Whether or not an individual will choose to purchase a personal copy will depend on how serious he is as a student of these ever-popular moths.

RICHARD S. PEIGLER, *Department of Entomology, Texas A & M University, College Station, Texas 77843.*

Bibliography of the Australian Butterflies (Lepidoptera: Hesperioidea and Papilionoidea) 1773–1973 by M. S. Moulds. 1977. Australian Entomological Press, Greenwich, N. S. W., Australia. 239 pp. US \$21.60.

Ever since the first sighting of a butterfly by Joseph Banks on the Australian continent in 1770 during Capt. Cook's first voyage, there has been a deep and abiding interest in Australia's endemic fauna. Along with the vast number of original descriptions, other major volumes have appeared, four in the last eight years. In 1932 Anthony Musgrave published the Bibliography of Australian Entomology, 1775–1930 through the Royal Entomological Society. Wisely, Maxwell Moulds in this present bibliographic work restricts the scope to butterflies and updates recent literature while adding some earlier works omitted by Musgrave.

This softback book is essentially divided into three main sections with a forward by I. F. B. Common. In the introduction Moulds outlines steps taken to compile this information which included a personal search through the literature to recheck original descriptions, punctuation, etc. He also chronicles a brief history of the Australian butterfly literature as well as the founding of various entomological societies.

The main section is simply titled "Bibliography" with references listed alphabetically by author's surname and with cross references in the case of more than one author. References for the author(s) are also listed chronologically by year with specific genera and species listed separately. New taxa are also indicated. Literature is cited only when the endemic taxa are discussed or in the case of taxa with a broad distribution, only when Australia is specifically mentioned. If some volumes have been reprinted, changes from the previous edition are indicated. The final section features a list of serial and journal abbreviations utilized.

When dealing within the confines of a bibliographic work, it is inevitable that some errors might surface, but I have found no major errors or omissions. There are a number of obscure references cited. However, in his effort to be as complete as possible, especially with the author's names, Moulds might have well been advised to have followed a more standardized format. There is, for example, a listing for the higher classification work on the Satyridae published in 1968 by Lee D. Miller. Moulds lists Dr. Miller's middle name as David, but it is actually a family name, Denmar. Thus this gives one a somewhat uneasy feeling about the credence of other middle names.

Despite this minor point, this bibliographic work is quite complete overall and a definite basic reference for all those interested in the Australian fauna.

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NORMAN DENBIGH RILEY 1890–1979
[Courtesy of the Trustees of the British Museum (Nat. Hist.)]

OBITUARY

Norman Denbigh Riley C.B.E. 1890–1979

Norman Denbigh Riley died 26 May 1979 after a long, exhausting illness. He had been with us as a friend and mentor for so long that it is hard to believe that we shall not see him again. He was born in London, 26 September 1890. Since his schoolboy days at Dulwich College, he was always interested in natural history, especially that of butterflies and moths. He was encouraged in this by the well-known lepidopterist Richard South, who lived next door to the Riley family in Balham, SW London. When he left school, Norman attended a course in Entomology at the Imperial College, where he found work as demonstrator to Sir Ray Lankester, then Director of the British Museum (Natural History). Two years later, in 1911, at the age of 21, he was appointed to the Museum Staff as Assistant, to work in the Department of Entomology.

In 1914 with the outbreak of the first World War, Norman joined the Army (RASC) serving in France and elsewhere. At the end of the war he was discharged, with the rank of Captain. He again took up his life at the British Museum where in 1932 he became head ("Keeper") of the Department of Entomology. Some years later, the accommodations in the Department obviously were inadequate, so the entire wing of the Museum was rebuilt, and the Department reorganized. The move into the new quarters was completed in 1952. This permitted the full expression of Norman's experience and originality. Both he and the official architect were largely responsible for the plans of the new wing.

He always was eager to acquire important material of every kind for the Museum, sometimes by purchase, but more often by gift. In these endeavors he was most successful. Today the scope of the collection is worldwide, forming part of an institution that is renowned internationally. The collections frequently are visited by entomologists from all over the world. Norman and his wife Edith were both extremely hospitable and they delighted in entertaining visitors from overseas at their house in Wimbleton, visits which will be remembered with gratitude by entomologists from many countries.

Norman was an excellent Committee-man, with an attractive and friendly personality. He was a good (and often witty) speaker. With his experience and ability, it is not surprising that he became involved in national and international entomological matters. He served as Secretary (1926–1928 and 1941–1951) and as Treasurer (1939–1940) to the Entomological Society of London. He was elected President in 1952. Norman was a charter member of the Lepidopterists' Society and served on the Council. He became Vice-president in 1954 and President in 1958. He also joined the Zoological Society (of London) and he had many friends among the active British zoologists.

As the years passed, Norman became associated with various projects which absorbed his restless energy. In 1923, on the retirement of Richard South, he became owner and editor of The Entomologist, at that time probably the most popular of the smaller entomological periodicals. It flourished under his direction. He remained sole editor for 36 years until his retirement in 1959. From 1950 until 1965 he served on the International Commission for Zoological Nomenclature, part of the time as Secretary, and as a member of the Editorial Committee. He was most active in the preparation of the present International Code.

In later years when he and I were closely associated over the publication of the book A Field Guide to the Butterflies of Britain and Europe, he remained intensely interested in all matters of nomenclature and emphatic over the strict application of the Code.

In his position as Keeper of the Department of Entomology at the British Museum, he was concerned with the International Congresses, most of which he was able to attend. He became Permanent Secretary for the Congresses in 1948, a most suitable appointment, in view of his flair for administrative work. A few years later, 1952, he was astonished and delighted to find himself appointed CBE on the Honours List, a

well-deserved distinction, in view of the time and effort he spent on matters of public interest.

The list of his scientific publications includes over 400 items on a wide variety of subjects. Many of these are comments on topical matters, reviews of books and meetings, etc., most of them published in his magazine, The Entomologist. He published many short descriptions of newly discovered taxa, usually Lycaenidae, his favorite butterfly family. His more important publications include the Field Guide to the Butterflies of the West Indies, the first modern collected account of the butterflies in these interesting islands, published by Collins, London, in 1975 when the author was aged 84!

LIONEL G. HIGGINS, *Chobham, Woking, Surrey, England.*

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of the collection and study of Lepidoptera. Contributors should prepare manuscripts according to the following instructions.

Abstract: A brief abstract should precede the text of all articles.

Text: Manuscripts should be submitted in *triplicate*, and must be typewritten, *entirely double-spaced*, employing wide margins, on one side only of white, 8½ × 11 inch paper. Titles should be explicit and descriptive of the article's content,including the family name of the subject, but must be kept as short as possible. The first mention of a plant or animal in the text should include the *full scientific name*, with *authors* of zoological names. Insect measurements should be given in *metric units*; times should be given in terms of the *24-hour clock* (e.g. 0930, not 9:30 AM). Underline only where *italics* are intended. References to footnotes should be numbered consecutively, and the footnotes typed on a separate sheet.

Literature Cited: References in the text of articles should be given as, Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and all must be listed alphabetically under the heading LITERATURE CITED, in the following format:

SHEPPARD, P. M. 1959. Natural selection and heredity. 2nd. ed. Hutchinson, London. 209 p.

——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10: 165–216.

In the case of general notes, references should be given in the text as, Sheppard (1961, Adv. Genet. 10: 165–216) or (Sheppard 1961, Sym. R. Entomol. Soc. London 1: 23–30).

Illustrations: All photographs and drawings should be mounted on stiff, *white* backing, arranged in the desired format, allowing (with particular regard to lettering) for reduction to their final width (usually 4½ inches). Illustrations larger than 8½ × 11 inches are not acceptable and should be reduced photographically to that size or smaller. The author's name, figure numbers as cited in the text, and an indication of the article's title should be printed *on the back* of each mounted plate. Figures, both line drawings and halftones (photographs), should be numbered consecutively in Arabic numerals. The term "plate" should not be employed. *Figure legends* must be typewritten, double-spaced, *on a separate sheet* (not attached to the illustrations), headed EXPLANATION OF FIGURES, with a separate paragraph devoted to each page of illustrations.

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Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes at this time will be charged to authors at the rate of 75ᶜ per line. A purchase order for *reprints* will accompany the proofs.

Correspondence: Address all matters relating to the *Journal* to the editor. Short manuscripts such as new state records, current events, and notices should be sent to the editor of the *News*: W. D. Winter, Jr., 257 Common Street, Dedham, Massachusetts 02026 U.S.A.

CONTENTS

JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

Michael Parsons

The object of the Lepidopterists' Society, which was formed in May, 1947 and formally constituted in December, 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

Membership in the Society is open to all persons interested in the study of Lepidoptera. All members receive the *Journal* and the *News of the Lepidopterists' Society*. Institutions may subscribe to the *Journal* but may not become members. Prospective members should send to the Treasurer full dues for the current year, together with their full name, address, and special lepidopterological interests. In alternate years a list of members of the Society is issued, with addresses and special interests. There are four numbers in each volume of the *Journal*, scheduled for February, May, August and November, and six numbers of the *News* each year.

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Order: Mail to Charles V. Covell, Jr., *Memoirs* Editor, Department of Biology, University of Louisville, Louisville, KY 40208, U.S.A.

The Lepidopterists' Society is a non-profit, scientific organization. The known office of publication is 1041 New Hampshire St., Lawrence, Kansas 66044. Second class postage paid at Lawrence, Kansas, U.S.A. 66044.

Cover illustration: Mature larva of *Ornithoptera goliath* Oberthür eating through the thick, corky stem of *Aristolochia crassinervia*, consuming the higher concentrations of secondary plant compounds that the stem of this vine contains. Original drawing by Mr. Michael J. Parsons, F.R.E.S., Hurst Lodge, Hurst Lane, Egham, Surrey TW20 8QJ, England.

IN MEMORIAM
Harry Kendon Clench

HARRY KENDON CLENCH
(1925–1979)

Journal of

The Lepidopterists' Society

OBITUARY

HARRY KENDON CLENCH

(1925–1979)

The world lost a great lepidopterist, and most of us lost a fine and true friend on the night of 31 March–1 April 1979. Harry K. Clench had just seated himself with a cup of coffee to watch the 11 p.m. newscast when he was stricken with a massive heart attack. He never regained consciousness and was pronounced dead at approximately 12:15 a.m. on 1 April.

Harry was born 12 August 1925 in Ann Arbor, Michigan, and shortly thereafter his family moved to Boston, Massachusetts, where he attended public schools. He came by his scientific inclinations honestly: his father, Dr. William J. Clench, is Curator Emeritus of mollusks at the Museum of Comparative Zoology, Harvard University. His late mother, Julia, supported his scientific career from its earliest manifestations. Harry became interested in butterflies while accompanying his father on land mollusk collecting trips throughout the eastern United States and the Bahamas, areas that were to intrigue him throughout his career. Another reason for Harry's decision to specialize on butterflies, rather than beetles or true bugs, was his acquaintance with Mr. Don Thomas, for whom *Hemiargus thomasi* Clench was described when Harry was in his teens.

Harry spent much of his formative years in the friendly confines of the MCZ, where he began his systematic work. One of those who influenced him greatly during the MCZ days was Vladimir Nabokov. He was the source of one of Harry's favorite stories on himself. Harry had agonized over a small *"Thecla"* from southern Brasil, and his frustration was well known to Nabokov. One evening Harry left the specimen in a box on his work bench, and went home; the following morning when he returned, Nabokov was nowhere to be seen, but the specimen had a neatly printed determination label on it from Nabokov proclaiming it to be *"Thecla caramba* Hewitson." One has

but to know how many Neotropical Theclinae Hewitson described (Comstock and Huntington's list had not yet been published) to imagine Harry's frantic search through the literature to find the original description of "*Thecla caramba.*" It is a tribute to Nabokov's puckish sense of humor that Clench never found the description he sought, because Hewitson wrote no such description. Harry, however, liked the name, and adopted it. It now stands as the valid name of a Neotropical thecline, despite the admonition of one of the elder Clench's Latin American graduate students: "You shouldn't use that name, Harry, it is just like calling your butterly '*Thecla Hell*'!"

Clench received his B.S. degree in Zoology from the University of Michigan in 1949, and his M.S. (Zoology) from the same institution two years later. He began work toward his doctorate, but in 1951 he accepted appointment as Assistant Curator of Entomology at Carnegie Museum of Natural History in Pittsburgh, Pennsylvania. He never completed his doctoral work. He was employed for the rest of his life at Carnegie, achieving the rank of Associate Curator in 1953, a title he held at his death.

During his tenure at Carnegie, Clench published more than a hundred papers (see Bibliography this issue) on the systematics, ecology and zoogeography of a variety of lepidopteran families. In his later years, however, he restricted himself increasingly to the Lycaenoidea and the butterflies of the Bahamian fauna. His major manuscript on the butterflies of the Bahamas is largely complete and will be published eventually.

It is with the Lycaenoidea of the New World and Africa that we most associate Harry Clench. His contributions to knowledge of the latter fauna are among the few American works on the butterflies of the fascinating Ethiopian region. His works on Neotropical hairstreaks, though far less extensive than we (or he) would have wished were of high quality. Many incomplete papers remained in his files, and these are now being completed so that these parts of Harry's work might be published. Examples of three such papers are included in this issue of the Journal.

Harry was involved in the publication of three butterfly books, two on North America and one on Africa. These were: the Theclini and Lycaenini in Ehrlich and Ehrlich (1961, How to Know the Butterflies), the Lycaenoidea in Fox et al. (1965, The Butterflies of Liberia); and as copy editor and author of major sections in Howe (ed.) (1975, The Butterflies of North America). With the exception of the forthcoming Bahamian manuscript, Clench's other booklength manuscripts are now lost to us.

In 1947, Harry married Odette M. Rigaud (now deceased), and had one daughter, Jocelyn (now Mrs. Hari Aas). Harry was divorced in 1967, and in the same year he married Dr. Mary Heimerdinger, Associate Curator of Birds at Carnegie Museum of Natural History, who survives him. Harry and Mary were field companions, as well as being together constantly in the home and the laboratory. Perhaps their best known expedition was during 1976 when they were part of the Carnegie Museum of Natural History Expedition to the Bahamas. There they searched for both butterflies and overwintering Kirtland's Warblers on many islands. The coverage they achieved suggested the feasibility of Harry's doing a book on Bahamian butterflies.

All members of the Lepidopterists' Society owe Harry debts of gratitude. He, with Charles and Jeanne Remington, founded the Society in 1947. Harry helped during the "bad old days" with stencil typing and mimeographing the first two volumes of the *Lepidopterists' News,* and generally aided in nursemaiding the Society from a struggling young entity to its present preeminent standing in the entomological community. Along with Theodore Sargent, Harry edited and generally ramrodded the *Commemorative Issue* (1977). In 1973–1974, Harry Clench served as President of the Lepidopterists' Society.

These professional details, however, imposing and impressive as they are, cannot convey a feeling of the man himself and his impact on others. Harry was an extremely warm and helpful person. He had strong affections, but at the same time he had equally strong dislikes: there was never a question as to how one stood with him. Some of his opinions, never hidden or unspoken, created animosity, but there was never a question about the honesty or consistency of his feelings. Attributes such as these instilled in those whom Harry liked, a sense of loyalty that was difficult for his detractors to understand.

And we, his friends, are stronger for having known Harry, and almost certainly we are better scientists because of his influence. He was a genius, with all that implies, but at the same time he was very patient with enthusiastic beginners (he certainly was with me!). Through his efforts we were guided into more scientific patterns of thinking. Harry would painstakingly go through drafts and the conclusions that we had reached, pointing out errors and new perspectives on the data we had obtained. Subsequent rewrites would receive the same careful attention. People with this kind of patience are all too few and far between.

Too many "authorities" convey the impression that they "do not suffer fools gladly" and go out of their ways to avoid contact with beginning students. God knows, there are too few competent people

in our field, and perhaps we should take more guidance from Harry and try to encourage the promising younger ones far more than we do. Ultimately, we, the professionals in the field, will have to be replaced, so why not have a say in *how* we will be replaced? I suspect that Harry had the answer, as he so often did.

Harry Clench's sense of humor, well known to his friends (who could forget his horrible puns?), became better known (anonymously) to the lepidopterological fraternity through his editing of *Frass, A Journal of Paralepidopterology.* When I was Secretary of the Lepidopterists' Society I often received irate letters from librarians wondering where their current "Pellets" of this august journal were. Such was the popularity of the publication, that in a year when Harry couldn't get out a number, the Secretary received an inordinate number of requests (yes, demands!) for copies.

It was this sense of humor that carried Harry through some very hectic field trips. He was in Mexico twice, in various parts of the U.S. many times, and in the Bahamas eight times. No expedition ever goes without "glitches," but Harry's capacity for laughter and seeing the best of a situation was infectious enough to carry him and anyone with him through trying times. He was one of the better field companions for just that reason; he knew when to work very hard and when to "roll with the punches," and this ability kept him from being "down." Tomorrow would always be a better day, and tomorrow would always produce better specimens.

Harry's favorite story about himself, and one that personifies both his sense of humor and his dedication to lepidopterology, concerned the time he went A. W. O. L., and wrote a paper in England during World War II. He had shipped out for Europe near the end of the War, contracted jaundice and later pneumonia on the voyage and eventually ended up in a hospital in Glasgow while his unit went to the Continent. When he recovered, he was sent to Tidworth Barracks for reassignment, but in typical Army fashion and since the War clearly was almost over, Harry's assignment was lost. He simply sat around the barracks, no one caring and no reassignment forthcoming. After a while Harry decided that he was just wasting his time, left the barracks *without* checking out and went to Tring, where the Lycaenidae from the British Museum (Natural History) were kept. He introduced himself, and happily settled into a routine of work (the resulting paper was later published in The Entomologist). Everything was going along well until one day Mr. N. D. Riley appeared on the scene (he was usually in London) and said that he understood that Harry was there without the blessing of the U.S. Army, and while they were

glad to have him there, his presence could prove embarrassing to the British Museum should he be caught. Harry replied that he hadn't really thought of it in those terms and that he would go back. When he returned to Tidworth Barracks, Harry was chagrined that he hadn't ever been missed.

Perhaps those at Tidworth Barracks had not missed Harry Clench, but those of us who now remain surely do! We will miss his astute scientific observations, his helping hand whenever we needed it and his ever-present wit. Most of all, however, we have lost an irreplaceable friend. Know, Harry, that we think of you often and fondly.

Lee D. Miller, *Allyn Museum of Entomology, 3701 Bay Shore Road, Sarasota, Florida 33580.*

TWO BOISDUVAL MANUSCRIPT GENERIC NAMES FIRST PUBLISHED BY LACORDAIRE IN 1833

In the first installment of a paper on French Guianan butterflies, Lacordaire (1833, Ann. Soc. Entomol. France 2: 379–397) introduced two generic names which had been used by Boisduval in manuscript. These names were not recorded by Hemming (1967, Bull. Brit. Mus. Nat. Hist. (Entomol.), Suppl. 9: 1–509).

The first such name is *Lucidia* (p. 387), which is valid and available, having as type-species (by monotypy) *Papilio albula* Cramer, 1776. A similar name (*Leucidia*) was introduced by Doubleday in 1847 (Gen. Diurn. Lep.: 77), for a different but related genus, indicating that it was a Boisduval manuscript name. Obviously, both *Lucidia* Lacordaire, 1833 and *Leucidia* Doubleday, [1847] were taken from the same Boisduval "label name," which probably had a variable spelling.

Lucidia Lacordaire (Pieridae) is considered here as a junior subjective synonym of *Eurema* Hübner, [1819].

The second name is *Peridromia*, which was given by Lacordaire (p. 392) to five nymphalids. I hereby designate *Papilio arethusa* Cramer, 1776, the last of the five species mentioned by Lacordaire, as the type-species of his genus *Peridromia*. By this action, *Peridromia* Lacordaire becomes a senior objective synonym of *Peridromia* Boisduval, 1836 (cf. Hemming, op. cit.).

Lt. Col. C. F. Cowan kindly advised me on this note.

Gerardo Lamas, *Museo de Historia Natural "Javier Prado," Universidad Nacional Mayor de San Marcos, Apartado 1109, Lima-100, Peru.*

AN ANNOTATED BIBLIOGRAPHY OF THE ENTOMOLOGICAL WRITINGS OF HARRY KENDON CLENCH
(1925–1979)

In the following bibliography I have examined all of the papers except those marked with an asterisk. Mrs. Jacqueline Y. Miller examined No. 20 for me. I received many papers from Clench and these all were marked with a serial number that corresponds with the numbers in the bibliography that he maintained. These numbers are not necessarily in order of publication but appear to be in the order in which he learned of their publication.

Clench's numbered bibliography that I have seen extends through his first 109 papers. In his curriculum vitae (on file in the Carnegie Museum) are listed, unnumbered, 37 papers from between 1943 and 1977. These are listed by year. With these two lists, my own series of numbered papers, a considerable number loaned to me by Dr. George Wallace (Emeritus Head of the Section of Insects and Spiders at the Carnegie Museum of Natural History in Pittsburgh, Pa.), the Zoological Record through the most recent issue for 1974, and the help of Dr. Lee D. Miller's incomplete file of Clench papers, the following was compiled.

At the time of his death Clench had several papers in various states of preparation. I will complete one that we had started in a desultory way. The others will be reviewed by Dr. Miller who will select those on which sufficient progress had been made to be sure of Clench's aim and opinion. These will be completed and published posthumously. Thus there will be a few papers in Clench's name beyond those already in editorial hands.

For each entry in the bibliography I have presented a number, year of publication, full title, citation of the place of publication and citation of Zoological Record (ZR) publication for papers noted there. For each new name proposed I have cited the name, type locality (t.l.) and repository of the type specimen. This should make the list a useful compendium of Clench's taxonomic work.

Without the help of Dr. Wallace and the encouragement of Dr. Miller this paper could not have been completed.

The repositories for Clench's types are noted at the end of each abstract:

AME—Allyn Museum of Entomology, Sarasota, Florida
AMNH—American Museum of Natural History, New York, New York
BM(NH)—British Museum (Natural History), London
BM(Tring)—British Museum at Tring, Herts.
CM—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
ZSM—Zoologische Staatssammlung, Muenchen, West Germany.

1941

1. Notes on two Bahama Lycaenidae, with description of a new subspecies. Torreia (Havana) No. 7, 7 p. *Strymon angelica dowi* n.ssp. (t.l. Arthurstown, Cat Island). Type in MCZ. ZR '43, No. 288
2. A new race of *Hemiargus* for the Bahamas. Mem. Soc. Cubana Hist. Nat. 15: 407–408. *Hemiargus catalina thomasi*, n.ssp. (t.l. Arthurstown, Cat Island). Type in MCZ. ZR '42, No. 275

1942

3. A new Bahaman *Eurema*. Mem. Soc. Cubana Hist. Nat. 16: 1–2. *Eurema chamberlaini banksi* n.ssp. (t.l. Smoky Point, Cat Island). Type in MCZ. ZR '42, No. 276
4. The identity of the Florida race of *Leptotes* (Lepidoptera: Lyaenidae). J. New York Entomol. Soc. 50:243–244. *Leptotes cassius theanus* Lucas is the proper name. ZR '42, No. 278
5. A new race of *Atlides halesus* Cramer from California (Lepidoptera: Lyaenidae). Entomol. News 53: 219–221. *Atlides halesus corcorani* f. "estesi" n. f. (t.l. Riverside, California). Note that Clench raised Gunder's ab. "corcorani" to the status of subspecies. Therefore the proper author for *A. h. corcorani* is Clench, not Gunder. Type of "estesi" in MCZ. ZR '42, No. 277

1943

6. The Lycaenidae of the Bahama Islands (Lepidoptera: Rhopalocera). Psyche 49: 52–60, "1942." *Hemiargus hanno filenus* (Poey) new comb., *Hemiargus bahamensis* n.sp. (t.l. Crooked Island); *Strymon acis armouri*, n.ssp. (t.l. Rum Cay); *Brephidium barbouri* n.sp. (t.l. Great Inagua Island). Types in MCZ. ZR '43, No. 291
7. Some new *Calisto* from Hispaniola and Cuba (Lepidoptera: Satyridae). Psyche 50: 23–29. *Calisto batesi* n.sp. (t.l. Loma del Torro, Dom. Rep.); *C. hysius montana* n.sp. (t.l. Mt. Basil, Haiti); *C. confusa debarriera* n.ssp. (t.l. Debarriere, Haiti); *C. herophile parsonsi* n.ssp. (t.l. Buenos Aires, Sta. Clara, Cuba); and *C. pulchella darlingtoni* n.ssp. (t.l. Constanza, Dominican Rep.). Types in MCZ. ZR '43, No. 292
8. A new *Axiocerses* from West Africa (Lepidoptera: Lycaenidae). J. New York Entomol. Soc. 51: 219–220. *Axiocerses harpax piscatoris* n.ssp. (t.l. Fisherman's Lake, Liberia). Type in MCZ. ZR '43, p. 166
9. A note on the Arizona *Erora* (Lepidoptera: Lycaenidae). J. New York Ent. Soc. 51: 221–223. The taxon *sanfordi* dosPassos is a subspecies of *quaderna*, not a synonym of it. ZR '43, No. 290
10. Two new species of *Incisalia* (Lepidoptera: Lycaenidae). Can. Entomol. 75: 182–185. *Incisalia henrici turneri* n.ssp. (t.l. Cowley Co., KN); *I. doudoroffi windi* n.ssp. (t.l. Placer Co., California). Type of *turneri* in MCZ, of *windi* in AMNH. ZR '43, No. 289
11. Some lycaenid aberrations (Lepidoptera: Lycaenidae). Ent. News 54:249–251. These are described but not named, six species are involved. ZR '44, No. 367

1944

12. Supplementary Notes on *Calisto* (Lepidoptera: Lycaenidae). Psyche 50: 115, "1943." *Calisto batesi* Clench 1943, a homonym of *C. hysius batesi* Michener, is renamed *C. micheneri*. ZR '43, No. 292A
13. Two new subspecies of *Everes comyntas* Godart (Lepidoptera: Lycaenidae). J. New York Entomol. Soc. 52: 59–61. *E. comyntas valeriae*, n.ssp. (t.l. nr. Lead, S.D.); *E. c. albrighti*, n.ssp. (t.l. Kings Hill, Montana). Types in MCZ. ZR '44, No. 368
14. Notes on Lycaenid butterflies. Bull. Mus. Comp. Zool. 94(6): 217–245.
    a. The genus *Callophrys* in North America, pp. 217–229, key to species and sub-

species, extended notes and description of *C. affinis washingtonia* n.ssp. (t.l. Brewster, Washington). Type in MCZ ZR '45.

b. The *acaste* group of the genus *Thecla*, pp. 229–245, key to the species, subspecies, extended notes, and descriptions of *T. agricola banosensis* n.ssp. (t.l. San Pablo, nr. Baños, Ecuador); *T. pseudolongula* n.sp. (t.l. Mapoto, Ecuador); *T. longuloides* n.sp. (t.l. Coroico, Bolivia); *T. longula* Hewitson (neotype locality Orizaba, Mexico): *T. legionis* n.sp. (t.l. Blumenau, Sta. Catarina, Brazil); *T. acaste catharinensis* [sic] n.ssp. (t.l. Sta. Catarina, Brazil); *T. portoena* n.sp. (t.l. Cusilluni, Bolivia); and, *T. marialis* n.sp. (Victoria, Mexico). Type of *banosensis* in AMNH, others in MCZ.

15. New neotropical Theclinae (Lepidoptera:Lycaenidae). J. New York Entomol. Soc. 52: 255–261. *Thecla caramba* n.sp. (t.l. Massaranduba-Blumenau, Brazil); *T. punona* n.sp. (t.l. Puno, Peru); and, *T. kalikimaka* n.sp. (t.l. Jalapa, Mexico). Type of *caramba* in AMNH, others in MCZ.

16. Two new subspecies of *Lycaenopsis pseudargiolus* Bdv. & LeC. J. New York Entomol. Soc. 52: 273–276. *L. pseudargiolus sidara* n.ssp. (t.l. Manitou, Colorado); and, *T. p. bakeri* (t.l. Baker, Oregon). Types in MCZ.

1945

17. Notes on the genus *Thaumaina* (Lepidoptera: Lycaenidae). Pan-Pac. Ent., 21: 14–16 (with R. G. Wind). *T. uranothauma delicisoa* n.ssp. (t.l. Wau, Morobe Dist., New Guinea). Type in MCZ.

1946

18. Notes on the *amyntor* group of the genus *Thecla* (Lepidoptera: Lycaenidae). Entomologist 79: 152–157, 185–191. *T. amyntor distractus* n.ssp. (t.l. Rio Minero, Muzo, Colombia); *T. detesta* n.sp. (t.l. Bogota, Colombia); *T. miserabilis* n.sp. (t.l. Rincon, Guerr., Mexico); *T. argentinensis* n.sp. (t.l. Tucuman, Argentina); *T. goodsoni* n.sp. (t.l. Tegusigalpa, Honduras); and, *T. acaste* f. "abnormis" n.f. (t.l. Tucuman, Argentina). Types of *distractus* and *detesta* in BM(Tring), others in BM(NH).

1947

19. The genus *Callictita* (Lepidoptera: Lycaenidae). Psyche 54: 57–61, (with R. G. Wind) *C. cyara arfakiana* n.sp. (t.l. Mt. Siwi, Arfak, Dutch New Guinea). Type in AMNH ZR '47, No. 3016

*20. New Indo-Australian Lycaenidae (Lepidoptera) Bull. Brooklyn Entomol. Soc. 42: 1–16 (with R. G. Wind, sr. author). *Candalides erinus stevensi,* n.ssp. (t.l. Way, Morobe Dist., New Guinea); *C. meeki kunupiensis,* n.ssp. (t.l. Mt. Kunupi, Menoo Valley, Weyland Mts., New Guinea); *C. grandissimi morobea,* n.ssp. (t.l. Wau, Morobe Dist., New Guinea); *Philiris diana papuanus* n.ssp. (t.l. Wau, Morobe Dist., New Guinea); *P. misimensis* n.sp. (Wau, Morobe Dist., New Guinea); *P. ariadne* n.sp. (t.l. Wau, Morobe Dist., New Guinea); *P. azula* n.sp. (t.l. Wau, Morobe Dist., New Guinea); *P. mayri* n.sp. (t.l. Mt. Siwi, Arfak Mts., New Guinea); *P. intensa birou* n.ssp. (t.l. Wau, Morobe Dist., New Guinea); *P. moira putih* n.ssp. (t.l. Pt. Moresby, New Guinea); *P. fulgens bicolorata* n.ssp. (t.l. Dobo, Aru Islands); *P. innotatus evinculis* n.ssp. (t.l. Redlynch, North Queensland, Australia). Types of *kunipiensis* and *mayri* in AMNH, of *putih* and *evinculis* in Cornell University, of *bicolorata* in R. G. Wind Collection, all others in MCZ. ZR '47, No. 3015

1948

21. Aberrations. Lepid. News 2: 6. Discusses the types of aberrations and applauds the growing tendency not to name them.

(No number) Notes on some Michigan butterflies. Lepid. News 2: 105.

(No number) Review: The butterflies of the District of Columbia and vicinity by A. H. Clark. Lepid. News 2: 108.

1949

22. Regional lists. Lepid. News 3: 15–16, A plea for publication of more such lists.

1950

23. Notes on Michigan Rhopalocera. Lepid. News 4: 14. New and unusual records.

1952

24. A new species of *Strymon* from Georgia (Lepidoptera: Lycaenidae). Amer. Mus. Novit. No. 1600, 19 pp, 3 figs. (with A. B. Klots, sr. author). *Strymon kingi* n.sp. (t.l. Savannah, Georgia). Type in AMNH. ZR '52, No. 1629

1953

25. New Indo-Australian Agaristid moths. Ann. Carnegie Mus. 33: 141–144. *Scrobigera* (?) *claggi*, n.sp. (t.l. Galog River, 6000 ft, Mt. Apo, Mindanao, Philippines); *Scrobigera umbrosa* n.sp. (t.l. "nr Manila", Philippines); *Argyropelidia megisto cissia* n.ssp. (t.l. Aru Islands); and, *Seudyra jordani* n.sp. (t.l. Lahum Mts., 5000 ft, Davao Prov., Mindanao, Philippines). All types in Carnegie Mus. ZR '54, No. 720

1954

26. The identity of *Crambidia allegheniensis* (Lithociidae). Lepid. News 8: 93–94. Redescription of Holland's type, which is a synonym of the European species *Eilema complana* (Linnaeus). ZR '54, No. 721

27. *Nymphalis californica:* A new record for Pennsylvania. Lepid. News, 8: 94.

28. Another case of a partially replaced lost vein in a new Nyctemerid from West Africa. Rev. Zool. Bot. Africa 50: 296–301, 1 fig. *Noctasota* n.g. *curiosa* n.sp. (t.l. Efulen, Cameroun). Type in CM. ZR '54, No. 722

1955

29. Review: The Lepidoptera of Pennsylvania. A manual, by H. M. Tietz. Lepid. News 8: 172–173.

30. A new species of the African genus *Pseudoarcte* Viette. Rev. Zool. Bot. Africa 51: 20–22, 2 figs. *P. albicollis* n.sp. (t.l. Efulen, Cameroun). Type in CM. ZR '55, No. 677

31. Revised classification of the butterfly family Lycaenidae and its allies. Ann. Carnegie Mus. 22: 261–274, figs. 1a–u. Includes Hamearinae, n. subfam. of Riodinidae (type *Hamearis lucina* [Linnaeus]); Helicopini, n. tribe of Riodinidae (type *Helicopis cupido* (Linnaeus)); Theopini, n. tribe of Riodinidae (type *Theope eudocia* Westwood). ZR '55, No. 674

32. Studies on the Limacodidae (Lepidoptera). 1. Notes on the African genera *Teinorhyncha* and *Ctenolita*. Ann. Mag. Nat. Hist. (12) 8: 153–159. Keys to species and description of *Teinorhyncha seydeli* n.sp. (t.l. Elizabethville, Congo Belge); *T. heringi* n.sp. (t.l. Kangewe, Ogove River, Gabon, French Equatorial Africa); *T. punctipes* n.sp. (t.l. Efulen, Cameroun); *T. kamerunica* n.sp. (t.l. Efulen, Cameroun). All types CM. ZR '55, No. 675

33. Studies on the Limacodidae. 2. A review of the African genus *Chrysamma*. Rev. Zool. Bot. Africa 52: 7–16, 6 figs. *C. purpuripulcra sudanicola* n.ssp. (t.l. Tembura, South Sudan); *C. amabilis* n.sp. (t.l. Efulen, Cameroun); and, *C. xanthocharis* n.sp. (t.l. Cholo, Nyassaland). Key to species. Type of *sudanicola* in Berlin Mus., all others in CM. ZR '55, No. 678

34. Some observations on the habits of *Strymon falacer*. Lepid. News, 9: 105–117, 3 figs, 3 tables. ZR '55, No. 676

1956

35. Contribution to the study of the neotropical Megalopygidae (Lepidoptera). 1. The genera of the *"Trosia"* group. Neotropica 2(7): 9–14, 13 figs. Key to genera. Two new genera noted: *Eochroma* (type *Trosia pulchella* Schaus); the other not named. ZR '58, No. 783

36. Notes on *Parabasis pratti*, a "mislaid" notodontid from New Guinea. Lepid. News 10: 15–17, 4 figs. Originally placed in Noctuidae and not mentioned since Bethune-Baker described it in 1904, the taxon proves to be a Notodonidae. ZR '56, No. 600

37. Lepidoptera Rhopalocera (Insecta) from Afghanistan. The 3rd Danish Expedition to Central Asia (Zoological Results 21). Vidensk. Medd. fra Dansk naturhist. Fren. 118: 141–192, 23 figs., 1 pl. (with Nicholas Shoumatoff). Satyridae: *Aulocera swaha parthicola* n.ssp. (t.l. Paghmann, 2000 m); *Kanetisa digna perdigna* n.ssp. (t.l. betw. Surtu and the top of Mt. Shah Fuladi, ca. 5000 m); *Satyrus pimpla tajik* n.ssp. (t.l. Mt. Shah Fuladi, 5000 m); *Pseudochazara mniszechii watsoni* n.ssp. (t.l. Kotal Pass, 3800 m); *P. porphyritica* n.sp. (t.l. Panjao, 2500 m); *Paralasa danorum* n.sp. (t.l. betw. Surtu and top of Mt. Shah Fuladi, ca. 5000 m); *Hyponephele capella jezail* n.ssp. (t.l. Panjao, 2500 m); *H. susurrans* n.sp. (t.l. Marak, 4500 m); *H. pulchella mussitans* n.ssp. (t.l. Puistagoli, 3500 m); *H. difficilis* n.sp. (t.l. Tarapas, 3000 m); Nymphalidae: *Melitaea paludani* n.sp. (t.l. Marak, 4500 m). Pieridae: *Colias shahfuladi* n.sp. (t.l. Takatu, 4500 m); *C. wiskotti sweadneri* n.ssp. (t.l. betw. Surtu and the top of Mt. Shah Fuladi, nr. 5000 m). Parnassiidae: *Parnassius delphius kohibaba* (t.l. betw. Surtu and top of Mt. Shah Fuladi, ca. 5000 m). All types in CM. ZR '56, No. 601

1957

38. New neotropical Cossidae (Lepidoptera). Ann. Mag. Nat. Hist. (12)9: 897–906, 9 figs., "1956." *Givarbela* n.g. *steinbachi* n.sp. (t.l. Prov. del Sara, Bolivia, 450 m); *Dimorphoctena* n.g. *egregia* n.sp. (t.l. Nova Linda, Rio Purus, Brazil); *Cossula* (s.l.) *morgani*, n.sp. (t.l. Mandeville, Manchester, Jamaica); *Citharalis* n.g. *idiosetoides* n.sp. (t.l. Prov. del Sara, Bolivia). All types in CM. ZR '57, No. 670

39. Notes on the occurrence of *Thymelicus lineola* (Hesperiidae) in North America: a summary. Lepid. News 10: 151–152. "1956" Records from Ontario, Michigan, New York and Ohio.

40. Two new records of Pennsylvania Lepidoptera. Lepid. News 10: 161–162, "1956." *Mnemonica auricyanea* (Walsingham), and *Erora laeta* (Edwards).

(No number) Common spring butterflies in the Ligonier Valley. Powdermill Educational Release (Carnegie Museum) No. 5, 2 p. mimeographed (June).

(No number) Unusual insects at Powdermill Nature Reserve. Powdermill Nature Reserve Educational Release No. 8, 2 p. mimeographed (Oct.).

*41. This summer's drought. Carnegie Mag. 31: 263–264, 274. (with O. E. Jennings, sr. author).

1958

42. Three interesting Lepidoptera from the Philippines. Ann. Carnegie Mus. 35: 69–76, "1957." *Delias levicki* Rothschild; *Danaus apoxanthus* n.sp. (t.l. Seliban River, 7000 ft, Mt. Apo, Mindanao); *Philippodamus* n.g. *jocelyna* n.sp. (Agaristidae) (t.l. Matuguinao, Samar Island). Types in CM. ZR '58, No. 780

43. Cossidae from Chile. Mitt. Muenchener ent. Gesell. 47: 122–142, 3 pls. *Givira leonera* n.sp. (t.l. La Leonera, Rancagua, Chile); *Philanglaus penai* n.sp. (t.l. Pichinachuel, 110–1400 m); *Philiodoron* n.g. *cinereum* n.sp. (t.l. La Leonera, 1700 m); *P. frater* n.sp. (t.l. Buchen, 1300 m); *Rhizocossus* n.g. *munroei* n.sp. (t.l. Caramavida). Types in CM. Pub. late December 1957? ZR '57, No. 671

44. Common spring butterflies at Powdermill. Carnegie Mag. 32: 122–124, 1 fig.
45. The "pumping" of certain moths at water. Lepid. News 11: 18–21, "1957." Noted for *Dysterus abortivaria* Herrich-Schaeffer and *Drepana arcuata* Walker.
46. The species of *Ethemia* (Ethemiidae) known from western Pennsylvania. Lepid. News 11: 44–45, "1957." *E. macelhosiella* Busck, a new record; *E. longimaculella* Chambers misdetermined as *zellariella* Chambers by Engel; first valid record.
47. Review: Colorado Butterflies. Part III. Libytheidae, Riodinidae and Lycaenidae, by Brown, Eff and Rotger. Lepid. News 11: 57–60, "1957."
48. Review: The butterflies of the Malay Peninsula, by Corbet & Pendlebury. 2nd ed. rev. enlarged by N. D. Riley. Lepid. News, 11: 60–62, "1957."
49. Synonymy of two African Euteliinae (Noctuidae). Lepid. News 214–215, "1957." *Caligatus angasii* Wing 1850, antedates *Pacadaria venustissima* Walker 1865. *Noctasota curiosa* Clench 1954, (see item 28), is a synonym of *Eutelia distorta* Hampson 1912, a Euteliinae, not a Nyctomeridae. ZR '58, No. 781
50. Review: Colored illustrations of the butterflies of Japan, by Mitsuo Yokoyama (rev. by Teiso Esaki). Lepid. News 12: 56.
51. Review: Colored illustrations of the insects of Japan, by Kichizo Takeuchi. Lepid. News 12: 56.
52. Review: Guia de Naturalista Sudamericanos, by Fontes & Parodi. Lepid. News 12: 56.
53. The butterflies of Powdermill Nature Reserve. Research Report No. 1, Powdermill Nature Reserve (of the Carnegie Museum). 11 p. mimeographed, no date.

1959

54. Review: Taxonomist's glossary of genitalia in insects, ed. S. L. Tuxen. Lepid. News 12: 125–126, "1958."
55. A new cossid moth from western China (Lepidoptera: Cossidae). Mitt. Muenchener ent. Gesell. 48: 82–85, 3 figs. *Sinicossus* n.g. *danieli* n.sp. (t.l. Omei-Shan, 7000 ft, Szechwan, China). Type in CM. ZR '58, No. 782
56. On the unusual structure and affinities of the Madagascan genus *Pseudocossus* (Lepidoptera: Cossidae). Rev. franc. d'Ent., Paris 26: 44–50, 2 figs. Redescription, ♂ genitalia of *P. uliginosus* figured. ZR '59, No. 747
*57. Powdermill Butterflies, 1959. Research Report No. 4, Powdermill Nature Reserve, a research station of Carnegie Museum, December, 1959. Mimeographed, 5 p. First supplement to item No. 53, above.
58. The Pseudarbelidae, a new family of Psychoid moths, with description of a new species from New Guinea. Tijdschr. Ent., Amsterdam 102: 223–229, 7 figs. Pseudarbelidae n.f., incl. *Casana* Walker, *Linggana* Roepke, *Pseudarbela* Sauber, and *Parazeuzera celaena* and *aurea* both Bethune-Baker and here placed in *Pseudarbela*. *Pseudarbela papuana* n.sp. (t.l. War [sic] Tami River, nr. Hollandia, Dutch New Guinea). Type in CM. ZR '59, No. 749.
59. The African genus *Macrocossus* (Lepidoptera: Cossidae). Veröff. Zool. Staatssamml. Muenchen 6: 3–8, ill. *Macrocossus coelebs* n.sp. (t.l. Okahandja, SW Africa). Type in ZSM; *M. caducus* n.sp. (t.l. Harbel, Marshall Terr., Liberia). Type in CM. ZR '59, No. 750
60. A collection of Cossidae (Lepidoptera) from South-west Africa. Veröff. zool. Staatssamml. Muenchen 6: 8–27, ill. Partial key to *Arcticossus*; *A. poliopterus* n.sp. (t.l. Brandberg, SW Africa); *A. tessellatus* n.sp. (t.l. Stamprict, SW Africa); *A. danieli* n.sp. (t.l. Wlotzkabaken, SW Africa); *Brachylia eutelia* n.sp. (t.l. Okahandja, SW Africa); *Phragmataecia andarana*, Okavango, SW Africa); *P. okavangae* n.sp. (t.l. Andara, Okavango River, SW Africa); *Xyleutes dictyotephra* n.sp. (t.l. Okahandja, SW Africa); *X. forsteri* n.sp. (t.l. Okahandja, SW Africa). Types in ZSM. ZR '59, No. 750
61. African Psychidae of the *Monda* group (Lepidoptera). Rev. Zool. Bot. Africa 60: 240–256, 4 figs. Key to *Monda* group; *Diaphanopsyche* n.g. *leucophaea* n.sp. (t.l. Efulen, Cameroun); *Dichromopsyche* n.g. *goodi* n.sp. (t.l. Metet, Cameroun). Types in CM. ZR '59, No. 748

1960

(No number) Tent Caterpillars. Powdermill Nature Reserve, Educational Release No. 30, 2 p. mimeographed.

62. A new subgenus and species of *Callophrys* (s.l.) from southwestern United States (Lepidoptera: Lycaenidae) Entomol. News 71: 137–144, 1 pl. (with P. R. Ehrlich, sr. author) *Sandia* n.g. *macfarlandi* n.sp. (t.l. La Cuerva Canyon, 6300 ft, W slope of Sandia Mts., Bernalillo Co., New Mexico). Type in AMNH. ZR '60, No. 885

63. Powdermill Butterflies, 1960. Research Report No. 5, Powdermill Nature Reserve, a research station of Carnegie Museum. 30 Dec. 1960. Mimeographed, 4 p. 2nd suppl. to Item 53, above.

1961

64. "Lycaeninae" in Ehrlich & Ehrlich, How to know the butterflies, p. 176–288, ill. (ZR '61, No. 957). *Chlorostrymon* n.g. (type *Thecla telea* Hewitson 1868); *Phaeostrymon* n.g. (type *Thecla alcestis* W. H. Edwards 1871); *Ministrymon* n.g. (type *Thecla leda* W. H. Edwards 1882); *Xamia* n.g. (type *Callophrys xami* Reakirt 1866); *Cyanophrys* n.g. (type *Strymon agricola* Butler & Druce 1872); *Euristrymon* n.g. (type *Thecla favonius* Smith 1797); *Hypostrymon* n.g. (type *Thecla critola* Hewitson 1874); and, *Electrostrymon* n.g. (type *Papilio endymion* Fabricius 1775). ZR '66, p. 338–340.

65. The *philobia* group of the genus *Cossula* (Lepidoptera: Cossidae). Ann. Mag. Nat. Hist. (13)3: 407–416, pl. 6, 6 figs. Key to the group; *Cossula wellingi* n.sp. (t.l. Chichen Itza, Yucatan, Mexico); *C. poecilosema* n.sp. (t.l. Prov. del Sara, Bolivia, 450 m); and, *C. eberti* n.sp. (t.l. Ouro Branco, Minas Geraes, Brazil). Types in CM. ZR '61, No. 647

66. "Lepidoptera" in the Encyclopedia of the Biological Sciences, ed. Peter Grey, Reinhold, New York. p. 556–559.

67. Notes on the genus *Thermonophas* (Lepidoptera: Lycaenidae). Ann. Carnegie Mus. 36(5): 49–62, 2 figs., 1 pl. A key to the species; *T. stempfferi* n.sp. (t.l. Batanga, Cameroun); *T. leucocyanea* n.sp. (t.l. Lolodorf, Cameroun). Types in CM. The generic name misspelled "Termoniphas" in ZR '65, p. 338. ZR '65, No. 851

68. A review of the African genus *Dapidodigma* (Lepidoptera: Lycaenidae). Ann. Carnegie Mus. 36(6): 63–67, 1 pl. Key to sp. and ssp.; *D. demeter* n.sp. (t.l. Efulen, Cameroun); *D. demeter nuptus*, n.ssp. (t.l. Kabongo, Katanga). Types in CM. ZR '65, No. 852

1962

69. *Panthiades m-album* (Lycaenidae): Remarks on its early stages and on its occurrence in Pennsylvania. J. Lepid. Soc. 15: 226–232, 9 figs. ZR '62, No. 711

70. *Satyrium behrii* (Lycaenidae) in Oregon. J. Lepid. Soc. 16: 44. Four records noted.

1963

71. Further notes on west African Lycaenidae (Lepidoptera). Entomol. News 74: 43–49. *Aphnaeus chapini occidentalis* n.ssp. (t.l. Efulen, Cameroun); *Anthene musagetes* (Holland) 1892 = *Anthene rubricincta* (Holland) 1891; *Cupidesthes brunneus* (Smith & Kirby) 1893 = *Cupidesthes paludicola* (Holland) 1891. Type in CM. ZR '63, No. 719

72. Review: The Lepidoptera of New York and neighboring states. Part IV, by W. T. M. Forbes. J. Lepid. Soc. 17: 40–42.

73. Notes on *Axiocerses* (Lepidoptera: Lycaenidae). J. New York Entomol. Soc. 71: 818–188, 3 figs. *Axiocerses harpax efulena* n.ssp. (t.l. Efulen, Cameroun); *A. h. ugandana* n.ssp. (t.l. Bugoma Forest, Unyoro, Uganda). Key to male genitalia. Types in CM. ZR '63, No. 720

74. *Callophrys* (Lycaenidae) from the Pacific Northwest. J. Res. Lepid. 2(2): 151–160,

1 table, 2 figs. (Dec. '63) *Callophrys sheridanii newcomeri* n.ssp. (t.l. Mill Creek, Yakima Co., 1800 ft, Washington). Type in CM.

1964

75. A synopsis of the West Indian Lycaenidae with remarks on their zoogeography. J. Res. Lepid. 2: 247–270, ill. "1963." Checklist. *Nesiostrymon* n.g. (type *Thecla celida* Lucas 1857); *Heterosmaitia* n.g. (type *Thecla bourkei* Kaye 1924); *Allosmaitia* n.g. (type *Thecla coelebs* Herrich-Schaeffer 1862).
76. Remarks on the relationships of the butterflies (excluding skippers) of the Cayman Islands. Occasional Papers in Mollusks 2(31): 381–382. Sept. 1964.
77. A new hairstreak for the United States. J. Lepid. Soc. 18: 189–190. *Oenomaus ortygnus* (Cramer) 1779, Brownsville, Texas, 14 Dec. 1962.
78. A new species of Riodinidae from Mexico. J. Res. Lepid., 3(2): 73–80, 6 figs. *Anatole rossi* n.sp. (t.l. ¼ mi ESE Ocozotepec, 1950 ft, Tuxtla Mts., Vera Cruz). Type in CM.
78A. How to prepare slides of sclerotized parts of Lepidoptera. Section of Insects and Spiders, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. (with Lee D. Miller). See item 118 for 2nd ed.

1965

79. Notes on some African Theclinae (Lepidoptera: Lycaenidae). J. New York Entomol. Soc. 72: 237–244, 2 figs. "1964" (Feb. 1965). *Iolaus vexillarius* (t.l. Batanga, Cameroun); *I. bolissus azureus* n.ssp. (t.l. Metet, Cameroun); *I. b. aurora* n.ssp. (t.l. Kyondo, Queen Elizabeth Park, Uganda); *I. aphnaeoides aethes* n.ssp. (t.l. Efulen, Cameroun). Types in CM. ZR '64, No. 510
80. Variation and distribution of *Hemiargus huntingtoni* (Lepidoptera: Lycaenidae). J. New York Entomol. Soc. 73: 41–45. *H. h. continentalis* n.ssp. (t.l. Minca, 2000 ft, Colombia); *H. h. hannoides* n.ssp. (t.l. Piste, Yucatan, Mexico). Types in CM. ZR '65, No. 854
81. Superfamily Lycaenoidea, in The Butterflies of Liberia, by R. M. Fox et al. Am. Entomol. Soc., Memoir No. 19, p. 267–403, figs. 163–233. Liptenidae: *Ptelina* n.g. (type *Pentila carnuta* Hewitson 1873); *Eresiomera* n.g. (type *Liptena isca* Hewitson 1873); *Tetrarhanis laminifer* n.sp. (t.l. Batanga, Camaroon); *T. simplex symplocus* n.ssp. (t.l. Harbel, Marshall Terr., Liberia); Iridanini, n. tribe (type *Iridana* Aurivillius); *Hypophytala* n.g. (type *Epitola hyettoides* Aurivillius 1895). Lycaenidae: *Spindasis crustaria mysteriosa* n.ssp. (t.l. 'Nzerekore, Guinea); *Athene amarah orphna* (t.l. Ganta Mission, Liberia). Riodinidae: *Abisara caerulea liberiana* n.ssp. (t.l. Ganta, Liberia). Types in CM. ZR '66, p. 29
82. A collection of butterflies from western Chihuahua, Mexico. Ent. News 76: 157–162. Made by C. H. T. Townsend in 1899. *Lycaeides meslissa mexicana* n.ssp. (t.l. Upper Rio Piedras Verdes, W. Chihuahua, Mexico, 7,100–7,300 ft). Type in CM. ZR '65, No. 853
83. African *Deudorix* (Lepidoptera: Lycaenidae): notes and descriptions. J. New York Entomol. Soc. 73: 178–181. Partial key to genus; *D. camerona katanga* (t.l. Elizabethville, Katanga); *D. nirmo* n.sp. (t.l. Efulen, Cameroun); *D. sadeska* n.sp. (t.l. Efulen, Cameroun); *D. laticlavia* n.sp. (t.l. Efulen, Cameroun). Types in CM. ZR '65, No. 855
84. A migration of *Libytheana* and *Kricogonia* in southern Texas. J. Lepid. Soc. 19: 223–224. Took place in July 1963.
85. The beginning of the butterfly season. J. Lepid. Soc. 19: 239–241. An attempt to quantify this phenomenon.

1966

NB. From 1966 through 1971 Zoological Record numbers were not assigned to each of the various papers cited in the Author Index.

(No number) Powdermill's missing butterfly. Powdermill Nature Reserve, Educational Release No. 62, 3 p. mimeographed, May 1966.

(No number) *Erora laeta*. Powdermill Nature Reserve, Educational Release No. 64, 4 p. mimeographed. June 1966.

86. The synonymy and systematic position of some Texas Lycaenidae. J. Lepid. Soc. 20: 65–70, 7 figs. *Strymon laceyi* (Barnes & McDunnough) 1910 = *Strymon alea* (Godman & Salvin) 1887; *Strymon facuna* Freeman 1950, not Hewitson 1877 = *Callophrys goodsoni* Clench 1946; *Thecla pastor* Barnes & McDunnough 1913, not Butler & Druce 1872 = *Callophrys miserabilis* Clench 1946. ZR '66, p. 29

(No number) It is not in the book. Carnegie Mag. Nov. 1966: 313–319, 3 figs. About a Mexican collecting trip.

1967

87. Behavioral thermoregulation in butterflies. Ecology 47: 1021–1034, 1 table, 1 fig. "1966."

88. A note on *Caria domitianus* and *ino* (Riodinidae), with description of a new species. J. Lepid. Soc. 21: 53–56, 2 figs. *Caria domitianus vejento* n.ssp. (t.l. Zacapa, Guatemala). *C. melicerta* Schaus 1890, is ssp. of *ino* Godman & Salvin 1886. Type in CM. ZR '67, p. 55

89. Further distribution records and taxonomic notes on *Philotes rita* (Lycaenidae). J. Lepid. Soc. 21: 141–142. Indicates possible n.ssp. from vicinity of Elko, Nevada. ZR '67, p. 55

90. New society and new journal. J. Lepid. Soc. 21: 140. Assoc. Minnesota Entomologists, and its Newsletter.

91. Type localities of some neotropical Lycaenidae taken by Gervase Mathew and described by W. C. Hewitson. J. Lepid. Soc. 21: 181–184. The following suggested type localities are based upon the logbook of "H.M.S. Repulse" upon which Mathew served: *Thecla sedecia* Mazatlan, Sinaloa, Mexico; *Thecla chonida* either Mazatlan, or Acapulco, Guerrero, Mexico; *Thecla cyrriana* either Callao or Paita, Peru; *Thecla critola* Guaymas, Sonora, Mexico; *Thecla mathewi* Acapulco, Mexico; *Thecla cyphera* either Isla Taboga or Ciudad Panama, Panama; *Thecla quadrimaculata* Valparaiso, Coquimbo or Arica, Chile; *Lycaena lyrnessa* Valparaiso, Coquimbo or Arica, Chile. Types should be in BM(NH). ZR '67, p. 55

92. Temporal dissociation and population regulation of certain Hesperiinae butterflies. Ecology 48: 1000–1006, 1 fig. A study of 11 flower-feeding species at Powdermill Nature Reserve of Carnegie Museum. ZR '67, p. 55

1968

93. The Mecoptera of Powdermill Nature Reserve. Powdermill Nature Reserve Research Report No. 20, 10 p. mimeographed. 14 species noted.

94. Revised list of Powdermill butterflies. Powdermill Nature Reserve Research Report No. 21, 9 p. mimeographed.

95. Some aspects of mating behavior in butterflies. J. Lepid. Soc. 22: 125–132. (with L. D. Miller, sr. author). Times of day and flying partner in mating are noted from observations and the literature, involving 12 pierids, 2 papilionids, 2 danaids, 15 nymphalids and 9 hesperids. ZR '68, p. 168

96. Butterflies from Coahuila, Mexico. J. Lepid. Soc. 22: 227–231. Report on collections made at three stations by Dr. C. J. McCoy and Mr. Arthur Bianculli incident to a June 1966 trip from the Carnegie Museum to study reptiles and amphibians. 38 species noted. ZR '68, p. 49

(No number) A spectacular fall migration of butterflies! Powdermill Nature Reserve Educational Release, No. 81, 2 p. mimeographed (Dec.).

(No number) A new butterfly from Powdermill. Powdermill Nature Reserve Educational Release No. 82, 3 p. mimeographed (*Hylephila phyleus*).

(No number) The strange case of the little sulphur. Powdermill Nature Reserve Educational Release No. 83, 2 p. mimeographed (Dec.).

1969

97. *Thecla viridis* Edwards 1862 (Insecta: Lepidoptera): proposal to place on the official list. Z.N. (S.) 1857. Bull. zool. Nomen. 25: 188–189. (with F. M. Brown, sr. author.) [January 1969] Zr '69, p. 29

98. Obituary: Thomas Herbert Elliot Jackson (1903–1968). J. Lepid. Soc. 23: 131–134. (with R. H. Carcasson, sr. author.) Brief biography and list of publications. ZR '69, p. 33.

1970

99. A new subspecies of *Brephidium exilis* from Yucatan (Lepidoptera: Lycaenidae). J. Lepid. Soc. 24: 3–6, 1 fig. *B. e. yucateca,* n.ssp. (t.l. Progreso, Yucatan, Mexico). Type in CM. ZR '71, p. 43

100. Generic notes on two hairstreaks new to the United States (Lycaenidae). J. Lepid. Soc. 24: 56–59, 1 fig. *Ocaria* n.g. (type *Thecla ocrisia* Hewitson 1868) for *ocrisia* from Alamo, Hidalgo Co., Texas. *Thereus* Huebner 1819 (= *Heterosmaitia* Clench 1964) *palegon* Stoll from the same locality. ZR '71, p. 43

101. Communal roosting in *Colias* and *Phoebis* (Pieridae). J. Lepid. Soc. 24: 117–120. *C. eurytheme* nr. Pittsburgh, Pennsylvania and *P. sennae eubule* at Horseshoe Beach, Dixie Co., Florida. ZR '71, p. 43

102. New or unusual butterfly records from Florida. J. Lepid. Soc. 23: 240–244, 1 table. *Eurema daira daira, E. d. palmira, Urbanus dorantes dorantes, Euphyes dion,* and *Poanes aaroni howardi.* ZR '71, p. 43

103. Sibling species in the *eurydice* group of *Lethe.* Psyche 77: 70–103, 22 figs. (with Ring T. Cardé, sr. author, and Arthur M. Shapiro). Detailed study of the distribution and differences in pattern. Establishes *L. appalachia* R. L. Chermock as a good species and *fumosa* Luessler as a ssp. of *eurydice* Johannsen. ZR '71, p. 37

1971

104. Some records of *Euristrymon ontario* (Lycaenidae). J. Lepid. Soc. 25: 80–82. Especially in the shale barrens of Virginia, Maryland and Pennsylvania. ZR '71, p. 43

105. Two new hairstreaks from Mexico (Lepidoptera: Lycaenidae). Bull. Allyn Mus., No. 3, 6 p., 2 figs. Key to species of *Micandra; M. dignota tongida* n.ssp. (t.l. El Encarnacion, Hidalgo, 2400–2450 m, Mexico); and *Panthiades m-album moctezuma* n.ssp. (t.l. Zimapan, 2140–2280 m, Hidalgo, Mexico). Type of *tongida* in AME and of *moctezuma* in CM.

1972

106. Review of the genus *Lasaia* (Riodinidae). J. Res. Lepid. 10(2): 149–180, 41 figs. "1971." Key to the species; *L. maria maria* n.sp. (t.l. Ajijic, 5300 ft, Jalisco, Mexico); *L. m. anna* n.ssp. (t.l. Ciudad Victoria, Tamaulipas, Mexico); *L. pseudomeris* n.sp. (t.l. San Jose de Chiquitos 300 m Sta. Cruz, Bolivia); *L. sula peninsularis* n.ssp. (t.l. Piste, Yucatan, Mexico); *L. aerugo* n.sp. (t.l. Llangua, Rio Llangua, Cajamarca, Peru); *L. agasilas callaina* n.ssp. (t.l. Ciudad Valles, San Luis Potosi, Mexico); *L. a. esmeralda* n.ssp. (t.l. Villarrica, Paraguay). ZR '71, p. 13 and ZR '72, No. 346.

107. *Celastrina ebenina,* a new species of Lycaenidae from the eastern United States. Ann. Carnegie Mus. 44: 33–44, 12 figs. Type locality Coalburgh, West Virginia. The type of *ebenina* is the lectotype of *nigra* ♂ W. H. Edwards in CM. ZR '72, No. 347

108. The boundary between *Satyrium liparops* and its subspecies *strigosum.* Ann. Carnegie Mus. 44: 11–24, 2 figs., map. ZR '72, No. 348

1974

109. The Bahamas: All this and Conch Stew. Carnegie Mag. May 1974: 204–209, ill. (with Mary H. Clench).

1975

110. A review of the genus *Hypostrymon* (Lepidoptera: Lycaenidae). Bull. Allyn Mus. No. 25, 7 p., 2 figs. Key to the species; *H. aderces* n.sp. (t.l. Comala, 2100 ft, Colima, Mexico); and, *H. margaretae* n.sp. (t.l. Urias, 2 mi S of Mazatlan, Sinaloa, Mexico). Type of *aderces* in AME, of *margaretae* in CM.
111. More on *Urbanus dorantes* (Hesperiidae). J. Lepid. Soc. 29: 106–107. Both *U. d. dorantes* and *U. d. santiago* are found on Grand Bahama Island.
112. The neotropical metalmark *Hermathena oweni* (Riodinidae): New records and major extension of the known range from Costa Rica to El Salvador and Mexico. J. Lepid. Soc. 28: 108–111, 2 figs. (with Thomas C. Emmel, sr. author, and Lee D. Miller). This high altitude species is now known as far north as Vera Cruz and Chiapas. *H. dativa* Schaus 1928, is a synonym of *oweni* Schaus 1913.
113. *Boloria toddi* or *bellona*? (Nymphalidae). J. Lepid. Soc. 29: 162. *Papilio belona* Fabricius 1775, has been given priority over *Papilio bellona* Cramer 1775, a pierid from South America. Therefore *bellona* Fabricius is available for the *Boloria* with *toddi* Holland 1928, as a ssp. and *ammiralis* Hemming 1933, as a synonym.
(No number) Miscellaneous contributions *in* "The alphabet butterfly coloring book for limerick loving lepidopterists," edited by Jo Brewer, [8] + v + 61 p., ill.
114. Editor of, and author of p. 1–72, introduction; p. 202–207, *Vanessa*; and p. 307–309, *Oenomaus, Thereus, Allosmaitia* and *Ocaria* in Butterflies of North America, W. H. Howe, illustrator and coordinator. Doubleday & Co., Garden City, New York. xiii, 633 p., 97 color plates.
115. Systematic notes on *Dryas iulia* (Heliconidae). J. Lepid. Soc. 29: 230–235. *D. i. largo* n.sp. (t.l. Key Largo, Florida). Clench divided the many subspecies into two groups, Antillean and continental, and presented a new synonymy accepting 13 subspecies.

1976

116. Fugitive color in the males of certain Pieridae. J. Lepid. Soc. 30: 88–90. The orange patch of androconial scales on the costal margin of the hind wing of *Nathalis iole* and the pink streak on the under forewing of *Eurema messalina blakei* found on freshly caught specimens disappears a few months after death.
117. *Nathalis iole* (Pieridae) in the southeastern United States and the Bahamas. J. Lepid. Soc. 30: 121–126. There are three continental segregates with different patterns of cold tolerance: southeastern, central and Pacific.
118. How to prepare slides of sclerotized parts of Lepidoptera. Section of Insects and Spiders. Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. (with Lee D. Miller) 2nd ed. See item 78A above. 6 p., ill.
119. In search of rare butterflies. Bahamas Naturalist 2(1): 2–8, ill. "Summer" 1976. Offset. The species notes are for *Apodemia carteri* Holland, *Battus devilliers* Godart and *Calisto sibylla* Bates.

1977

120. A list of the butterflies of Andros, Bahamas. Ann. Carnegie Mus. 46: 173–194, map. Comments on 59 species known from the island.
121. Butterflies of the Carnegie Museum Bahamas Expedition, 1976. Ann. Carnegie Mus. 46: 265–283. 22 islands were visited and butterflies were collected on 19 of them. A total of 1003 specimens representing 54 species, were taken between 26 February and 4 April. Five taxa were new to the islands: *Wallengrenia druryi, Eurema elathea, Anartia jatrophae saturata, Anaea verticordia* and *Heliconius charitonius churchi*.

122. *Papilio aristodemus* (Papilionidae) in the Bahamas. J. Lepid. Soc. 32: 273–276. *P. a. driophilus* n.ssp. (t.l. Cat Island); *P. a. bjorndalae* n.ssp. (t.l. Great Inagua Island). Types in CM.
123. The names of certain Holarctic hairstreak genera (Lycaenidae). J. Lepid. Soc. 32: 277–281. *Fixenia* Tutt, 1907, to be used for *favonius, ontario* and *polingi*; *Satyrium* Scudder 1876, for the other 12 nearctic species usually placed in this genus.
124. Butterflies of Clench's western collecting trip 1977. Xeroxed. 15 p. Limited circulation. Stations 396 through 454, mostly in New Mexico.

1978

125. The Lepidopterists' Society Commemorative Volume 1945–1973. Compiled by Roy O. Kendall. Edited by Harry K. Clench and Theodore D. Sargent. In addition HKC contributed the Foreword, p. vii–xiii, and was coauthor of "A Backward Glance—A Glimpse Ahead." p. 15–19.
126. Butterflies of the Turks and Caicos Islands: A preliminary list. Mimeographed with limited circulation. 4 p. 32 species noted.

1980

127. Butterflies of Great and Little Inagua, Bahamas (with Karen A. Bjorndal, jr. author.) Annals of Carnegie Museum, 49: 1–30, A detailed history of collecting on these remote islands and a full report on about 1000 specimens representing 34 species from Great Inagua and 240 specimens representing 17 species from Little Inagua. *Epargyreus zestos inaguarum* Clench & Bjorndal, n.ssp. (t.l. Matthew Town, Great Inagua); two undescribed ssp. are noted.
128. How to make regional lists of butterflies: some thoughts. J. Lepid. Soc. 33: 216–231.
129. Book Review, "Butterflies of South Australia" by R. H. Fisher, 1978, Handbooks Comm. of South Australian Gov't. J. Lepid. Soc. 33: 268–269.

At the time that the above was compiled there were several manuscripts either in the hands of editors or being prepared by Dr. Lee D. Miller. (Three additional papers appear in this issue of the *Journal*.) Dr. Mary H. Clench checked the above against Clench's record cards of his publications and supplied the numbers for items 122–126. In addition to the above listed serious contributions to entomology Harry Clench christened, wrote, edited and circulated *FRASS, An Occasional Journal of Paralepidopterology*. It was issued in "pellets"—1973, 1974, 1975 and 1976. These four-page publications are inspired writing.

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HARRY KENDON CLENCH, IN THE FOUNDING OF THE LEPIDOPTERISTS' SOCIETY

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Harry Clench has, for more than thirty-five years, been one of the most supportive and warmly interactive American lepidopterists in this century. His early passing means the sad ending of his encouragement and expert advice for the circle of lepidopterists in the Pittsburgh region who could visit with him in person regularly, and for the very large number of correspondents who had the good fortune to receive in the mail his occasional bonanzas of fascinating answers and ideas.

Harry's point of view on interchanges between lepidopterists was never more productive than in 1946 and 1947 when he and I worked out the organization of the Lepidopterists' Society and produced the early issues of the *News.* As his brief and very nice foreword to the recent Society *Commemorative Volume* makes clear, he and I were in total agreement on the guiding principle of the new Society's operation, as stated in our letter of 24 March 1947 inviting 325 lepidopterists to join:

". . . facilitating the exchange of specimens and ideas by both the professional worker and the interested amateur in the field."

Harry's foreword tells some of the early story, but there is much more of importance, and I would like to add a little more background now. As Harry reported, his father William J. Clench and my father P. Sheldon Remington were youthful collecting pals in the Boston area. There was a third friend, Kendall W. Foster, who often joined them in collecting trips for Lepidoptera and for mollusk shells. The three were protégés of Charles W. Johnson, the noted zoology curator at the Boston Society of Natural History, and they got their advice on collecting locales and techniques from Mr. Johnson and regularly went to him for help in identifying their specimens. It was fitting that when Bill and Julie Clench chose a middle name for their first-born son, Harry, they produced a fusion, "Kendon," from the names of Kendall Foster and Sheldon Remington. Just think, Harry might have carried Remster, Foston, Sheldall, or even Shelster instead of Kendon! W. J. Clench became a widely respected curator of malacology at the Harvard Museum of Comparative Zoology, P. S. Remington became a preparatory school headmaster and teacher of mathematics, Latin, and biology at the Principia and Daycroft

Schools, and K. W. Foster also went into prep school teaching of biology, at the Groton School. Only Dr. Foster gave up specimen collecting, for the study of marine fish coloration. Harry's father and mine not only stayed in close touch, they actually went on at least two mollusk-collecting expeditions together, especially aimed at getting a substantial research collection of freshwater mollusks from the swift rivers in the Tennessee Valley that were about to be disastrously altered by the great series of T.V.A. dams. Some of the mollusks are now extinct, and that magnificent Clench-Remington collection is mainly divided between the museums of the Universities of Michigan and Yale. Harry and I were too young to join these trips in the late twenties, but I'm sure he heard a lot about Shel, and I certainly heard many tales of Bill. Our first direct contact came by mail when we found that each of us by incredible coincidence began our publishing almost simultaneously with papers on species of the same small genus of Blue butterflies. His was "A new race of *Hemiargus* for the Bahamas," apparently published in late December 1941. Mine was "The distribution of *Hemiargus isola* (Reakirt) east of the Mississippi River," published early in 1942!

So in June of 1946, when I was to arrive with my new Californian bride in Cambridge, Massachusetts, after my three years of military service as a medical entomologist, it was natural that my father wrote to his Cambridge friend Bill Clench for help with our apartment hunting. Harry came home from military service with his French bride at about the same time, and of course we immediately became close friends. The senior Clenches were wonderfully hospitable, and on many weekends Jeanne and I were evening guests in their home. Harry and I were soon incubating plans for the birth of the Lepidopterists' Society (which we at first called "The Lepidopterists' Union"). Harry accurately recalled these steps in his foreword, mentioned above. I don't remember that one of us first thought of the idea of a society and then convinced the other. Probably we had both mused on it before we met, like the accident of our simultaneously doing manuscripts on *Hemiargus* with no shared knowledge.

Due to my intensive Ph.D. program at Harvard, we had to work nights and weekends on the organizing, and on the writing, mimeographing, and mailing of the *News*, and when Harry began serious studies at the University of Michigan several months after the *News* was started, his move forced him to give up all regular work on the *News* and Society. But our collaboration in the crucial early period was intensive and warmly mutual. In retrospect, we occasionally have recalled our view that the Society was an idea whose time had come, and that no doubt without our efforts one or more other organizations

resembling it would soon have been founded in North America. But we felt that our special role was in finding a style for this society, directed at advanced amateurs and professionals together, and was better than various alternatives that might have been created. We had a few negative critics, but gratifyingly few, and I believe that Harry's felic- itous personality contributed to the friendly reception we met.

CALLOPHRYS (MITOURA) HESSELI (LYCAENIDAE) IN GEORGIA: A STATE RECORD

It has long appeared likely that *Callophrys hesseli* Rawson & Ziegler occurs in Georgia, particularly in light of recent records for this species in northern Florida (Nordin, News Lepid. Soc. 1978(2): 9; Roman, News Lepid. Soc. 1979 (2): 12). Since the larval foodplant of *hesseli* is the white cedar (*Chamaecyparis thyoides* L.), we have sought the insect for the last several years in the only area of Georgia where white cedar is known to occur. This covers a four-county area (Marion, Schley, Talbot and Taylor) through which Cedar Creek and Whitewater Creek flow. The best stands of white cedar were in several swamps along the Taylor and Schley county lines.

On 7 April 1979 at 1100 h, at the crossing of Georgia Hwy. 127 and Whitewater Creek, we took a fresh female *C. hesseli*. It had alighted on the fresh shoots of a willow (*Salix longipes* Shuttl.), some six feet from a white cedar growing on the creek bank. It was the only *hesseli* we were able to net that day, although we saw numerous hairstreaks in flight and at rest at or very near the top of the cedars—hopelessly out of reach of our nets—both at this location and several others in the area. We find it curious that some of these hairstreaks on the white cedars were *Callophrys gryneus* Huebner. While we saw substantial numbers of red cedars (*Juniperus virginiana* L.) along the highways, we wonder if perhaps *C. gryneus* uses *Chamaecyparis thyoides* as well as *J. virginiana* as a larval foodplant.

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HARRY KENDON CLENCH: A REMEMBRANCE

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In June of 1943 I received a telephone call from a professor in Boston asking me if by any chance his son was in Caldwell visiting us. My response was that he was not here. Nevertheless early the next morning there was a knock on our front door and we met Harry Clench for the first time. He had hitchhiked from his home in New England to Caldwell, Kansas. We asked him how he found our house so early in the morning (it was still dark) and he replied "I walked down the street until I found a house that smelled of paradichloro-benzene."

At that time Viola and I were interested in the "hair-streaks" and had corresponded with Harry for some time about them. We were interested in doing some serious study of the group, but had little knowledge of how to approach such a study. At that time Harry's knowledge of research methods was limited, but he knew a number of knowledgeable lepidopterists in the east, who were experienced in research. Several days later, after a number of telephone calls we acquired a working knowledge of some basic methods in research. Soon Harry, Viola and I were busy dissecting specimens, counting scales on the wings and joints of antennae along with other things that had been suggested to us. Nothing revolutionary resulted from these efforts but all three of us acquired a basic knowledge of how to conduct such a study. Harry, particularly, went on to develop himself in the area of such research, with the result of a major contribution to the science.

Harry was fascinated with the midwest and stayed in Caldwell a number of weeks. He found it hard to believe that nearly every family (in 1943) had a motor vehicle for transportation. He secured a job with a friend of ours, working in the harvest fields. His first paycheck went for a "cowboy" hat—a black felt hat, as I recall.

Viola's brother, JE, was home on furlough from paratroop training. In the evenings all of us sat on the front porch (this was before air-conditioners) and talked of butterflies, collectors and how to get in touch with other lepidopterists to make exchanges. It was an enjoy-able spring, even with a war hanging over our heads.

Some evenings our discussions became a bit exotic as we discussed such things as creating a Lepidoptera Science Center where all knowledge of each species of butterfly or moth would be recorded on a card index, so that anyone could call for that particular card and

immediately have a reference to all knowledge on that species—shades of the computer. Other evenings our conversations were more prosaic and turned to practical means of making contacts with collectors over the world for exchange of specimens and ideas. As I recall the exchange of ideas was secondary. Still it was during these conversations that the idea of a Lepidoptera organization began to crystallize. While the idea of an organization jelled, nothing was done—but the idea remained alive in Harry's mind, for after the war when he met Charles Remington, they renewed the idea and between them the Lepidopterists' Society was born.

THE REDISCOVERY OF *LIBYTHEANA TERENA* IN JAMAICA (LIBYTHEIDAE)

Libytheana terena (Godart) (considered a subspecies of *L. carinenta* by some) has been reported with certainty from the island of Jamaica only once; Philip Gosse collected a single male at Alligator Pond (Manchester Parish) in the latter half of June 1846 (Gosse 1851, A naturalist's sojourn in Jamaica, London; Brown & Heineman 1972, Jamaica and its butterflies, London; Riley 1975, A field guide to the butterflies of the West Indies, London). Avinoff & Shoumatoff (1946, Ann. Carnegie Mus. 30: 263–295) report a sight record at Balcarres (Portland Parish).

On 17 July 1977 one of us (GV) captured a single specimen approximately 3 km W of Mandeville (Manchester Parish, elev. ca. 650 m). This specimen, sex undetermined, is in the senior author's collection. About 200 m from the location of this first capture, GV observed another specimen, which eluded capture, on 11 Sept. 1977.

GV subsequently captured three additional specimens, all males, at the Mount Forest Christian Youth Camp, 18 km S of Mandeville (elev. ca. 450 m), approximately 8 km from Gosse's Alligator Pond locality: a fresh male on 23 May 1978, and two worn males on 2 July 1978 (all three deposited in the Natural History Museum of Los Angeles County).

These captures demonstrate the continued existence of *Libytheana terena* in Jamaica, more than 130 years since the last (and first!) valid record. It remains to be seen, however, whether the species is resident on Jamaica, or whether recolonization occurs periodically from Hispaniola, the only other island where it is known to occur.

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PAPILIO LADON CRAMER VS. ARGUS PSEUDARGIOLUS BOISDUVAL AND DECONTE (LYCAENIDAE): A NOMENCLATORIAL NIGHTMARE

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ABSTRACT. A general discussion of pertinent portions of the International Code of Zoological Nomenclature is given, especially of those parts dealing with names proposed from erroneous localities by the early authors. An example is given of Plate 270 of Pieter Cramer's De Uitlandsche Kapellen . . . , and the taxa described therein are figured. Cramer's representations are compared with actual specimens. The problem of the identity of *Papilio ladon* Cramer, described from "Kaap de Goede Hoop" is discussed, and it is determined that it is a senior synonym of the Nearctic *Argus pseudargiolus* Boisduval and Leconte. A neotype is designated for *P. ladon* (TL— Patuxent River, Anne Arundel Co., Maryland). The taxonomy of the New World *Celastrina argiolus* group is discussed.

"The objects of the Code are to promote stability and universality in the scientific names of animals . . . ." (International Code of Zoological Nomenclature, preamble)

But are these objectives being achieved? When one looks at interminable name changes and taxonomic squabbles over the proper choice of names for taxa, one wonders about the efficacy of the present Rules.

One of the cornerstones of all versions of the Code is the "Law of Priority," which states that the oldest name for a taxon is *the* valid name for that entity. This basic regulation is one of the most unpopular among taxonomists—perhaps a well-known name would be upset by a previously undiagnosed and unidentified earlier name. Human beings resist change of familiar patterns. For this reason, the International Commission on Zoological Nomenclature from time to time suspends the Law of Priority and validates more recent names that are in wide use. This does not always happen, so nomenclature is subject to the possibility of a change, which is contrary to the quotation above.

Suspension of the Law of Priority belongs to the Plenary Powers of the Commission. These powers are not invoked haphazardly: there

must be a real question of whether or not the aims of "stability and universality" will be served by such action. Names thus validated are placed on the appropriate Official List and are accepted without further question. Unfortunately, the procedure is ponderous, uncertain and discouraging to many taxonomists. Even though the names thus conserved or rejected are not always the "right" ones, they are the then "legal" names—in taxonomy, as in other aspects of life what is "right" may not be "legal." Since they have at least the look of "order," rather than "chaos," such lists are useful and are the rules of the "game" that taxonomists accept.

During the past several years, there have been attempts to circumvent the use of senior synonyms on the basis of disuse during the preceding fifty years, or some like time. Fortunately, codifying such a procedure has been defeated but this philosophy reemerges with almost every revision of the Code. The present revision is no exception. While the controversial Article 23b of the 1964 Code was finally repealed in 1973, a similar proposal is incorporated into the present draft, although it requires that the Commission invoke its Plenary Powers. The problem with such an approach, appealing as it first appears, is that *many groups of animals are not even mentioned* during a given fifty-year period. In such a case, *all* of the names could be "unused senior synonyms"! Further, senior synonyms, even when pointed out by authorities, are occasionally ignored and revert to "unused senior synonym" status. Such a "conspiracy of silence," then, may be deemed correct.

It is argued that return to "unused senior synonyms" would wreak havoc with the nomenclature. Such is simply not the case—for a few years, at the most, such "new/old" names are confusing, but the scientific community rapidly becomes accustomed to their use. Several cases among North American butterflies demonstrate the point:

Pyrgus oileus. Perhaps the most easily accepted of these resurrections is the ascension of *Pyrgus oileus* (Linnaeus, 1767: 795). This species was described from a specimen from "Algeria" and rarely (Humphreys & Westwood, 1841: pl. 38) was applied to a New World insect. The American species was named *Papilio syrichtus* by Fabricius (1775: 534), and two Fabrician specimens still exist in the Kiel collection. This butterfly was known as *syrichtus* for many years, until Evans (1953: 221) resurrected the name *oileus* for it based on the type specimen in the collection of the Linnaean Society of London. Subsequent authors have accepted this nomenclatorial change without quibbling.

Specimens that are figured along with the original description are rather easy to accept. Cases of this kind have produced the majority

of applications of "unused senior synonyms." Two examples will suffice:

Polites coras (Cramer, [1775]: 51; Pl. 31, Fig. F). This name was forgotten throughout most of its history—presumably because it was described from "Surinam." Later, W. Kirby (1837: 300) described this insect as *Hesperia peckius*, and the Cramerian name was forgotten until 1917 when Barnes & McDunnough listed as a synonym of *peckius* (p. 21) "?*coras* Cr." A little later, Draudt (1924: 932) used the name *coras* for the first time as a senior synonym of *peckius*, an action that was not taken seriously until Evans (1955: 332) used the name in preference to the then-familiar *peckius*. Cramer's ([1775]: Pl. 31, Fig. F) insect, in addition to being described from "Surinam" is so badly figured that it is referable to the Nearctic insect only by the use of a great deal of imagination! Despite the shortcomings of both the verbal description and the figure of the type, acceptance of the name *coras* in precedence to *peckius* has been rapid and complete—many younger lepidopterists would no longer know what was being referred to by "*Polites peckius*" without having to think a bit and equate that name with the now-familiar *coras*.

Hyllolycaena hyllus (Cramer, [1775]: 67–68; Pl. 43, Figs. B–C). This species was described from "Smirna," and for many years it remained in the literature as an unknown copper from the Palearctic. Meanwhile, Guérin-Ménéville ([1831]) and Boisduval and Leconte ([1833]) independently (?) redescribed both sexes of the beast as *Polyommatus thoe*, a name that was used for the species almost universally until Brown & Field (1970) unsnarled the nomenclatorial tangle and resurrected the name *hyllus* for our North American butterfly. That decision is now accepted by nearly all taxonomists (e.g., Opler, 1975: 312 and Miller & Brown, 1979: 15–17). Such acceptance in less than ten years belies the idea that nomenclature will be hopelessly upset by resurrection of "unused senior synonyms"—one must admit that taxonomists are either an adaptable or a gullible lot. We would prefer to believe the former.

The third method of resurrecting "unused senior synonyms" is perhaps the least satisfactory. In this case, no specimen or published figure exists, and the description itself is so vague that it could apply to almost any species. Most such cases are, regrettably, also mislabelled as to locality. The mechanism for validating these names seems less than satisfactory, based more on assessment of the work of the modern taxonomist than on evaluation of the merits of the case. The Hesperiidae again offer us some superlative examples: when one reads the original descriptions of *Hesperia origenes* Fabricius (1793: 328, described from "Indiis") and *Hesperia aesculapius* Fabricius

(1793: 347, described from "America boreali"), it is difficult to asso-
ciate the names with the once-familiar *Polites manataaqua* (Scudder,
1863: 175) and *Amblyscirtes textor* (Hübner, [1827]–[1831]: Figs.
515–516), respectively. No type-specimens exist for either species,
and Evans (1955) rather arbitrarily assigned the names to North Amer-
ican species; nonetheless, it is a tribute to the regard held for Evans'
work that these names, once pointed out by him, have become uni-
versally accepted. We suggest that names based on poor descriptions
and not accompanied by plates might be better candidates for
suppression under the Plenary Powers of the I. C. Z. N. than others
accompanied by figures.

Quality of Plates in *De Uitlandsche Kapellen*

Cramer's early plates, especially those published between [1775]
and [1778] were reasonably good representations of the insects they
pictured. Later, as Cramer approached death, the quality of the plates
was much less satisfactory. Even at best, though, Cramer's illustra-
tions of small butterflies were little more than caricatures, frequently
unrecognizable ones at that.

At the height of production of *De Uitlandsche Kapellen* Cramer
would do a drawing indicating what he wanted to show, and other
artists would copy the shapes and colors to the best of their abilities.
Perhaps an "assembly line" approach was taken, with Cramer "rough-
ing out" the plate, then other artists adding this or that color until the
job was completed. This was a time-honored procedure among illus-
trators, but it is troublesome to assign work to a specific artist—the
most we can say about the plates in *De Uitlandsche Kapellen* is that
they were done by "the school of Pieter Cramer." We shall never
know who did what in these illustrations. No two of the sets of hand-
colored plates are exactly alike, and for this reason, it is necessary to
consult more than one copy of Cramer to begin to get a "feel" for
what he meant to show. The other avenue of determining what Cra-
mer had in mind is to consult the pattern plates that are now in the
possession of the British Museum (Natural History).

Small insects were frequently illustrated slightly larger than life-
size, and wing shapes are sometimes inaccurate (usually the apex is
more rounded than natural), but his representations of maculation are
generally correct. In the plates, the colors are frequently about right
for the insects reproduced.

Reliability of Data in *De Uitlandsche Kapellen*

Many of the species described by Cramer in *De Uitlandsche Ka-
pellen* were based on specimens brought to him by seafarers, and

Cramer accepted their locality labels as correct. This procedure caused Cramer to describe a sizable minority of his species from the wrong localities and/or zoogeographic regions. This is not especially strange, since Cramer was dealing with what he thought were immutable species created by God, and the Creator could place closely allied species anyplace He wanted. It has caused us difficulty, though, and whereas most of these mislabelled species have been assigned correctly to extant material, others have not been and remain either forgotten species or species assigned to the erroneous localities as "lost" species.

It is not surprising, then, that several North American butterflies were described from the wrong localities—in fact, it would have been amazing if it were otherwise. A quick look through the Cramerian names yields such spurious type-localities as "Smirna," "Indiis," "Cape of Good Hope," etc. Such widely disparate localities did not bother the older workers, but they do disturb us. Such things must be taken in context.

Difficulties such as those outlined in this section and the last have made Cramer's species difficult to identify. Nevertheless, recognition of the conditions under which Cramer worked should help in the identification. Many such determinations have been made already, and it is to be hoped that the others can be done speedily.

Butterflies in Cramer's Plate 270

Cramer's Plate 270 of *De Uitlandsche Kapellen* was published posthumously by Caspar Stoll. The date assigned is [1780] (I. C. Z. N., Opinion 516, 1958), and this information has been placed on the Official List of Works . . . as of 1958. This plate obviously suffered from the absence of the "master" and is more of a caricature than are many in the work. This plate is reproduced (Fig. 1). A look at the insects represented on the plates and comparison with actual specimens is informative.

Figures A and B represent the type specimen of *Papilio mesentina* Cramer, an insect now equated with *Papilio aurota* Fabricius (1775: 197); this butterfly is presently placed in the genus *Belenois*. The Cramerian insect is a male from the "Coromandel," probably "Kaap de Goede Hoop," and we illustrate (Figs. 2–3) a male from South Africa of *B. aurota*. Cramer described the species on Plate 270 from the van Lennep collection the remains of which are now contained in the British Museum (Natural History), via the Rothschild collection. The forewing in the Cramer figure is not as acute as an actual specimen, and the under surface of the hindwing is ochreous yellow in the plate but only very faintly overlaid with yellow scales in the most
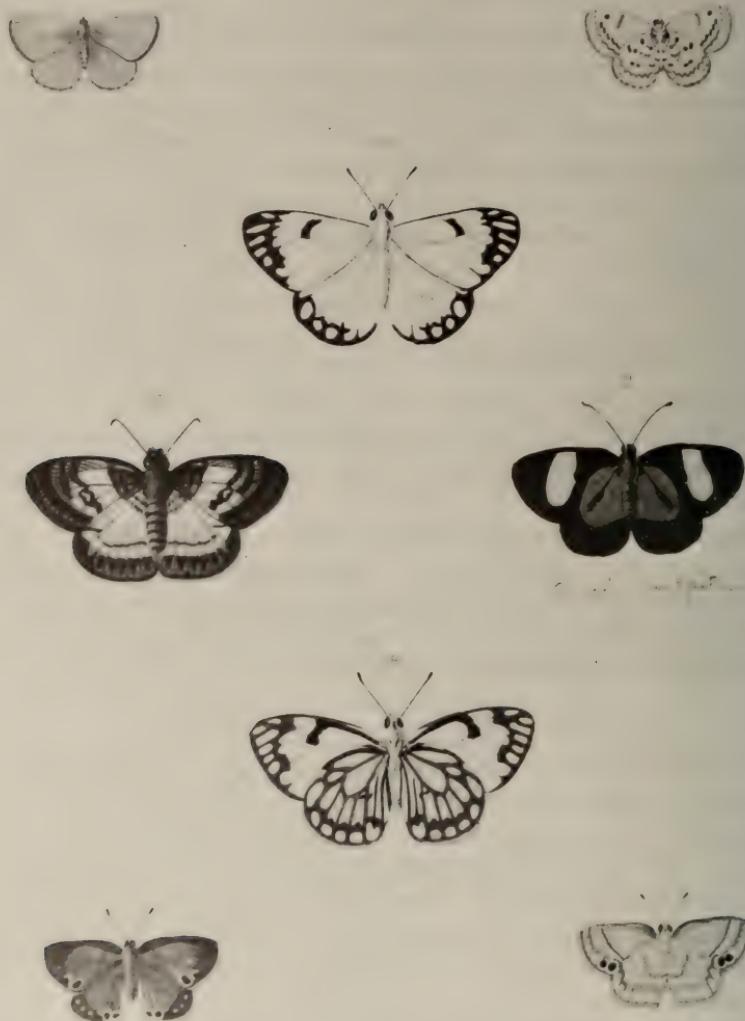
FIG. 1. A copy of Cramer's Plate 270 from *De Uitlandsche Kapellen*, vol. 3 [1780]. The identities of the species figured are discussed in the text, and the handwritten determination under Fig. C was done by Dr. Ellison A. Smyth, Jr.

yellow specimen we could find. Nevertheless, because the type-locality is corrected, it is easy to associate *mesentina* with *aurota*.

Figure C represents the type of *Papilio epitus* Cramer from "Surinam." This species is presently assigned to the genus *Orimba*, and
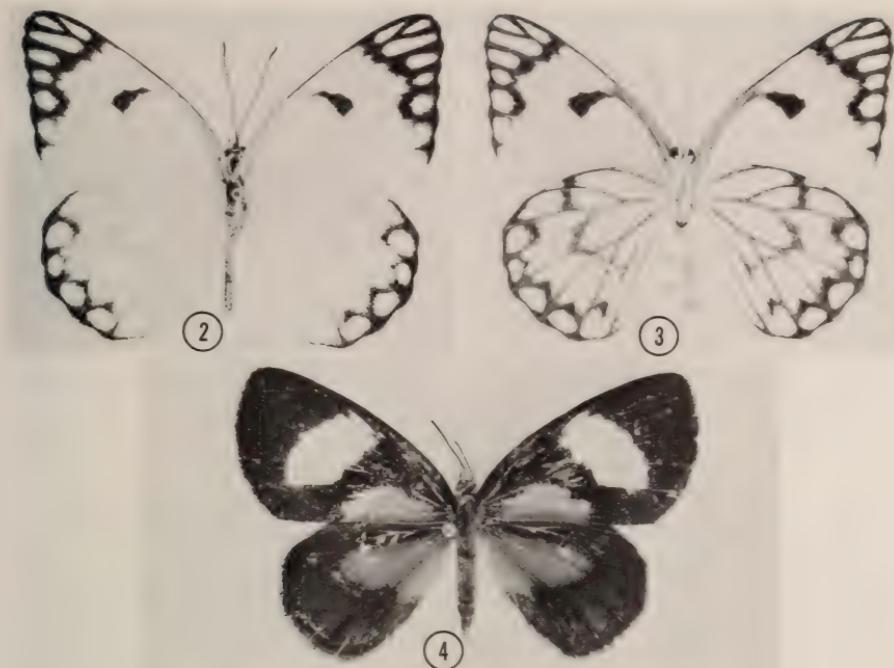
FIGS. 2–4. Species illustrated by Cramer [1780]: Plate 270. **2–3,** *Belenois aurota* (Fabricius), ♂, upper (2) and under (3) surfaces; REP. SOUTH AFRICA: TRANSVAAL: Struben's Valley, 13.xii.1970 (W. Henning) (Allyn Museum photos 031080-1/2). **4,** *Orimba epitus* (Cramer), ♀, upper surface; GUYANE FRANÇ.: St. Jean du Maroni (LeMoult colln.) (Allyn Museum photo 031080-5). All specimens in this and other plates in the collection of the Allyn Museum of Entomology.

the type is a female (the male is blue above). Only the upper surface is illustrated by Cramer, and we illustrate a female (Fig. 4) from French Guiana for comparison. The illustration is perhaps the most accurate of any on this plate, but the specimen is larger than any female of *epitus* that we have seen, and the forewing apex is more rounded.

Figures F and G are of *Papilio iolaus* Cramer, described from the Cape of Good Hope. This insect is now considered a synonym of *Papilio lara* Linnaeus (1764: 320) and is a member of the genus *Leptomyrina*. We illustrate a representative male from South Africa (Figs. 5–6) of *L. lara* for comparison. The forewing of the illustrated specimen is rounder than that of a specimen, and Cramer overemphasized the markings of the hindwing.

Figure H is of *Papilio melander* Cramer, a South American hesperiid that is now synonymous with *Papilio menippus* Fabricius
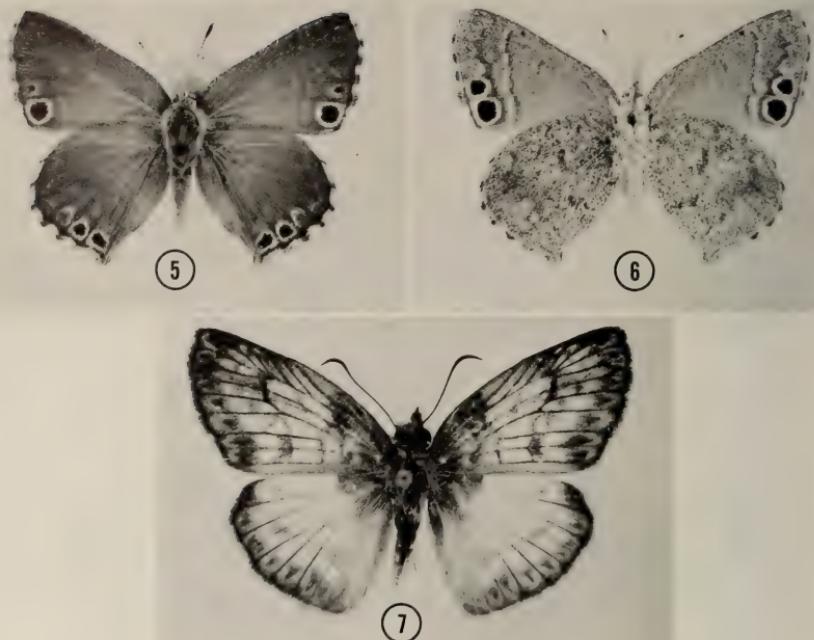
Figs. 5–7. Species illustrated by Cramer [1780]:Plate 270. **5–6,** *Leptomyrina lara* (Linnaeus), ♂, upper (5) and under (6) surfaces; REP. SOUTH AFRICA: CAPE PROVINCE: Oudtshoorn. 2.xi.1966 (J. C. McMaster) (Allyn Museum photos 031080-7/8). **7,** *Mylon menippus* (Fabricius), ♂, upper surface; BRASIL: GUANABARA: Leblon, 2.ii.1971 (C. Callaghan) (Allyn Museum photo 031080-3).

(1776: 292), a member of *Mylon*. We here illustrate a representative *M. menippus* (Fig. 7, upper surface only). The forewing of Cramer's representation is again too rounded, and the markings are badly caricatured. The size is a bit too large, even though *menippus* is a fairly large skipper.

Figures D and E represent the type specimen of *Papilio ladon*, a name used later in the same volume (Cramer [1780]: 164; pl. 284, fig. G) for an Indo-Malayan skipper now considered synonymous with *Badamia exclamationis* (Fabricius) (Evans, 1949: 72). It was described from "Kaap de Goede Hoop," and the figure definitely represents some polyommatine blue. Examination of South African lycaenids (Dickson, 1978) reveals no very close matches for *ladon*. The most similar are *Azanus j. jesous* (Guérin-Ménéville) and *A. natalensis* (Trimen), but both of these species have prominent subapical bars on the forewing beneath, characters that would have been em-

phasized rather than ignored, by Cramer. Consequently, we must look elsewhere than the Cape region of South Africa to find *ladon*.

The title of Cramer's work suggests we must look beyond the confines of Europe for *ladon*. We must examine the shipping routes that seafarers might have taken and ports that they might have visited, for such adventurers supplied Cramer with his material. Captains in the slave trade stopped at such places as Capetown, Sierra Leone, Surinam, Jamaica and one or another ports in Colonial America (New York, Savannah and possibly ports on Chesapeake Bay) and supplied many of the specimens. Other captains of Cramer's acquaintance sailed to the Dutch East Indies (now Indonesia) and brought back many specimens, especially from Amboina (Ambon) and Java. In these places, then, we must search for what *ladon* might represent.

The Identity of *Papilio ladon* Cramer

Ménétriés (1857: Pl. 10, Fig. 5) labelled his illustration as "*Lycaena ladon* var.," an insect from Japan that de l'Orza (1869: 20) later named as *Lycaena ladonides*. That butterfly is now known to be a member of the *Celastrina argiolus* complex. Certainly both Ménétriés and de l'Orza saw at least a hint of *Celastrina* in the original illustration of *Papilio ladon*.

Celastrina is a genus, unfortunately, whose range encompasses many of the areas from whence Cramer received material, but it is not found in the Cape region of South Africa. Nevertheless, it has been necessary to examine representatives of the group from the Holarctic and Indo-Malayan regions to determine which (if any) of the species *could* be the true *ladon*. Discussion with Col. J. N. Eliot at the British Museum (Natural History) suggested several *Celastrina* that approximated Cramer's figure of *ladon* (insofar as one could!). Most of the Indo-Malayan "look alikes" are found in the foothills of the Himalayas, an area from which Cramer was unlikely to obtain specimens.

Most Indo-Malayan *Celastrina* with well-patterned under surfaces are deficient for consideration as *ladon*. Many (*puspa* Moore, and relatives) have white areas on the upper surface of one or both wings; other species are too purplish-blue to qualify (the type of *ladon* is supposed to be caerulean blue). Other *Celastrina* are blue enough, but they have broad margins on the forewings, and often on the hindwings as well. Most of the species in the Indo-Malayan region fail on the wider margin criterion; the only one close to Cramer's figure is *C. limbata* (Moore), and that species is too purplish on the upper surface (D'Abrera, 1977: 381).

We must, then, look to the New World for *ladon*. Scudder (1889:
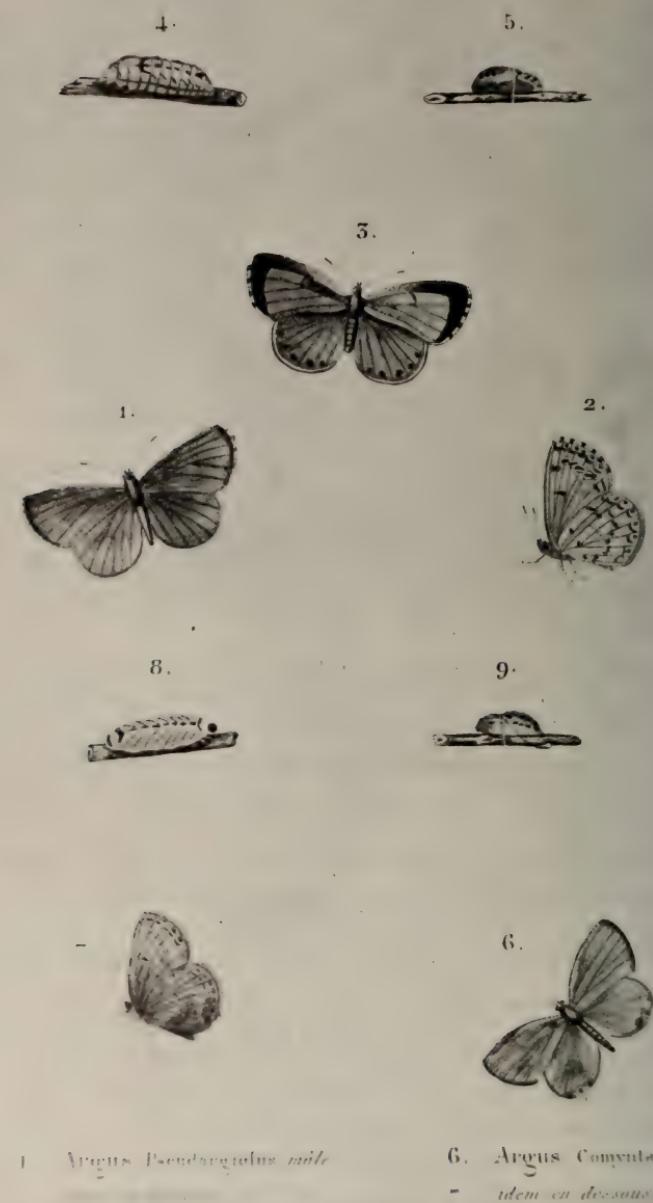
FIG. 8. A copy of Boisduval and Leconte's plate 36 from *Histoire Lepidoptères* ... *Amerique septentrionale*. [1833]. Figs. 1–5 represent *Argus pseudargiolus*.
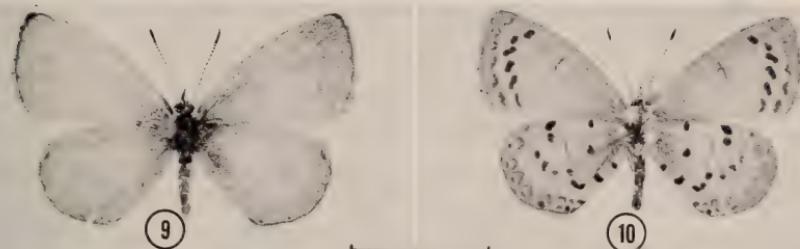
FIGS. 9–10. *Papilio ladon* Cramer, Neotype ♂, upper (9) and under (10) surfaces; MARYLAND: Anne Arundel Co.: Patuxent River, 19.iv.1964 (W. H. Evans). See text for designation. Scale represents 10 mm.

928) may have been the first to associate this name with the familiar *Celastrina pseudargiolus* (Boisduval & Leconte [1833]: 118–119; Pl. 36, Figs. 1–6, as *Argus p.*), stating in his discussion of *pseudargiolus*, "Not *Papilio argiolus* Linn., but possibly *Pap. ladon* Cram." A few later authors (for example, Dyar, 1902: 45, and Draudt, 1921: 818) went a step further and used *ladon* in preference to *pseudargiolus*.

Although Cramer's renditions of maculation are overdone, he had an "artist's eye" for colors. Assuming this is so with *ladon/pseudargiolus*, we can restrict Cramer's specimen to a spring brood individual from the Middle Atlantic States. The under surface maculation is heavy (not so heavy as Cramer illustrates), and the upper surface is uniformly sky blue with narrow dark margins. The size of the illustration cannot be taken literally—Cramer often exaggerated the size of small butterflies, presumably to obtain the details of maculation that he wanted. The differences in markings between Cramer's illustration (Fig. 1) and that of Abbot (redrawn in Boisduval and Leconte [1833]: Pl. 36) (Fig. 8) are insignificant when one recognizes Cramer's overemphasis of the dark markings.

Spring specimens from New England and montane New York and Pennsylvania usually are referable to the forms "lucia" (W. Kirby) and "marginata" (W. H. Edwards), but further south specimens approach the pattern shown by Cramer's illustrations. By the time one reaches Georgia, spring brood specimens are too pale to be referable to *ladon* with certainty. A specimen that conforms to the Cramerian figure is here illustrated (Figs. 9–10).

Later in the spring, and during the summer, individuals from later broods are much paler beneath with finer markings; on the upper surface males of these broods frequently show some white. Both the

Cramer and the Boisduval and Leconte plates, then, represent spring specimens.

Is the North American *Celastrina*
Conspecific with *argiolus*?

For years it has been fashionable to equate North American animals with their Palearctic counterparts. This "modern" thinking has pervaded taxonomic thought and has aided elucidation of some intriguing ideas. In a few instances, however, such thinking has obfuscated natural relationships and, indeed, caused spurious affinities to be accepted. Each case must be reexamined strictly on its own merits.

For the past thirty years most systematic workers have accepted all North American *Celastrina* as subspecies of the Eurasian *C. argiolus* (Linnaeus, 1758: 483), a species of undeniable kinship to the American insect. This relationship, or lack thereof, was one of the aspects of *Celastrina* taxonomy that we wished to examine when we began our review of the group some twenty years ago, and it soon became apparent to both of us that while *argiolus* and "*pseudargiolus*" were very close, it took imagination to state that they were conspecific. Some interesting patterns (that were confusing if viewed according to the "conventional" logic of the day) began to emerge: 1) the androconial scales differed between New and most Old World *argiolus*-group butterflies; 2) the male genitalia showed some intriguing differences and 3) *argiolus* in its several Old World subspecies has an iridescent dusting of blue-green scales near the base of the under hindwing, whereas "*pseudargiolus*" and the Japanese *ladonides* either do not show this characteristic, or it is very weak. *C. ladonides* is an anomalous Palearctic insect, most closely resembling Nearctic material and perhaps representing an eastern Palearctic subspecies of the American "*pseudargiolus*." We argued long and hard over *Celastrina* taxonomy before finally Clench (1972) described *C. ebenina*. Incidentally, *C. ebenina* is much less distinct from "*pseudargiolus*" than either is from *argiolus*.

The valvae of *argiolus* (Fig. 11) are rather different from those of *ladonides* (Fig. 12), *ladon/pseudargiolus* (Fig. 13) or the Mexican-Central American *gozora* (Boisduval, 1870: 17) (Fig. 14), especially regarding the shape of the distal process and the extent of the dorsal process. The dorsal process is simple in *argiolus* and all of its putative subspecies, but it is progressively more bilobate in the other taxa, distinctly so in *gozora*. The distal process is shorter and rather contorted in *argiolus*, but straighter and more evenly curved in the other populations. If these populations are subspecies, they are very far along the path of speciation.
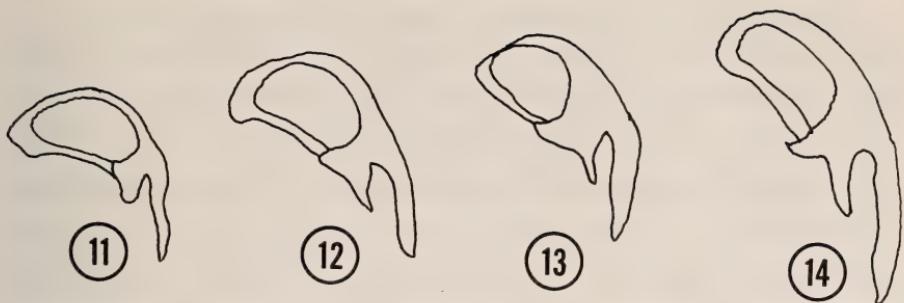
FIGS. 11–14.   Inner faces of valvae of selected *Celastrina*. **11,** *C. argiolus* (Linnaeus). **12,** *C. ladonides* (de l'Orza). **13,** *C. l. ladon* (Cramer). **14,** *C. ladon gozora* (Boisduval).

A possible nomenclatorial solution to the *argiolus*-group problem was put forward by Amadon & Short (1976). These authors may be criticized for "dodging" the fundamental species *vs.* subspecies argument, but by so admitting a degree of uncertainty, they cannot be accused of dogmatism. Much of the rhetoric surrounding circumpolar species vs. subspecies *is* dogmatic, and perhaps a system that immediately states assumed relationships at the outset will serve to elucidate relationships better than either conventional approach.

Using the Amadon-Short system, *argiolus* becomes a "superspecies" and is denoted as "*Celastrina [argiolus]*." The allopatric taxa within a superspecies that are accorded specific ranking are known as "allospecies," and in the case of *Celastrina* are denoted as "*Celastrina [argiolus] argiolus* (Linnaeus)" (Palearctic); "*Celastrina [argiolus] ladonides* (de l'Orza)" (Japan, Korea); "*Celastrina [argiolus] ladon* (Cramer)" (most of North America) and *Celastrina [argiolus] gozora* (Boisduval)" (SW U.S. through Central America).

There is some doubt as to the status of the latter name, however, since *cinerea* (W. H. Edwards) occasionally interbreeds with more definite *ladon* populations. This eventuality can be accounted for by assuming that the allospecies *gozora* is an extremely differentiated subspecies of *ladon*, in which case *gozora* would be a "megasubspecies" and denoted as "*Celastrina (ladon) gozora* (Boisduval)." Note that an allospecies is tied to its superspecies with the latter's name in square brackets; a megasubspecies is written about as normally, but the species epithet is in parentheses. This megasubspecies (if it is one) is more distinct from the eastern *ladon* than is *echo* (W. H. Edwards), the latter taxon being written as "*Celastrina ladon echo* (W. H. Edwards)." The only problem then is, to which species do we assign *cinerea*? If one considers *gozora* an allospecies, it would be

"*Celastrina gozora cinerea* (W. H. Edwards)"; if *gozora* is a mega-subspecies (it must be one or the other), the name becomes "*Celastrina ladon cinerea* (W. H. Edwards)." This scheme, complicated as it seems, gives a shorthand for elucidating complicated relationships.

Our conclusion, then, is that *Celastrina argiolus* is a superspecies with a single New World allospecies, *ladon*. C. [*argiolus*] *ladon* is divided into at least one megasubspecies, *gozora*, and a plethora of subspecies. This idea can be transferred profitably to many other American Rhopalocera, especially the Hesperiidae. Evans (1955: 124–125) lists *Monca telata* (Herrich-Schäffer) with three subspecies, *tyrtaeus* (Plötz), *telata* (Herrich-Schäffer) and *penda* Evans. Bell (1941: 183–185) made a very strong case for the distinctness of *tyrtaeus* and *telata*, based on genitalic differences and moderate sympatry. *M. telata* would seem to be a classic example of a superspecies, and *tyrtaeus* (which gets into southern Texas) could profitably be denoted "*Monca* [*telata*] *tyrtaeus* (Herrich-Schäffer)." A similar solution could be employed with the *Hesperia comma* complex, a knotty problem for treatment by "conventional" means.

Celastrina ladon (CRAMER)

For the reasons given in the preceding sections, we contend that the proper name for the North American *Celastrina* is *ladon* (Cramer, [1780]). The Nearctic and Old World members do not appear to be conspecific, even though they are mutual closest relatives. Further, the name *pseudargiolus* (Boisduval & Leconte, [1833]) is a junior synonym, the two names both based on spring brood material. Boisduval and Leconte's name was proposed for a specimen (or specimens) presumably from Georgia, and Cramer's specimen probably came from further north: nevertheless, material from both places are subjectively placed as belonging to the same subspecies, as well as species.

The problem, then, is straightforward: shall we accept a long-used junior synonym, or shall we invoke the Law of Priority in favor of the older Cramerian name? To those who would advocate the former course, we can say that invoking priority for a long-used junior synonym need not cause the confusion that some authors claim. Cases in point are many among North American butterflies, and in all cases where the older name is used, it is accepted by the lepidopterological community in short order. Who but the older lepidopterists now remember "*Euptychia eurytus*" (*Megisto cymela*), "*Polites manataaqua*" (*Polites origenes*) or "*Polites taumas*" (*Polites themistocles*)? Still, these were the accepted names fifty years ago for those three butterflies, and there are similar cases scattered through the North American Rhopalocera, plus countless others in the moths. Lepidop-

terists, and scientists in general, are adaptable and do not cling to erroneous beliefs (or names) for long, once the error is pinpointed.

We have attempted to find a type specimen of *Papilio ladon* Cramer by searching and requesting that searches be made. Unfortunately, the type appears to be no longer extant. Since it must have come from the Atlantic Coast, one can pinpoint the exact locality no nearer than the Mid-Atlantic States, perhaps as far north as New York City. Examination of material at hand suggests that the area near Baltimore, Maryland might be a prime candidate for a type-locality. We have found a single early brood male from that area that satisfies most of the criteria emphasized in Cramer's original plate. This specimen is designated as the Neotype of *Papilio ladon* Cramer, as follows:

Neotype   a specimen in the Allyn Museum of Entomology is hereby designated as the Neotype of *Papilio ladon* Cramer. It bears the following labels: a handlettered label "14 April 1964/Patuxent River/Anne Arundel/Co., Maryland" (specimen collected by William H. Evans); a machine-printed label, "A. C. Allyn/Acc. 1970-48" and a partly printed, partly *handwritten* label, "Allyn Museum Photo/No. *031080-9/10*." To these labels we have added a fourth, a red label printed and *handwritten* in black, proclaiming the specimen's status: "NEOTYPE ♂/Papilio ladon/Cramer, [1780]/ designated by/ *H. K. Clench & L. D. Miller*, 1980."
    This specimen is here figured (Figs. 9–10). Its forewing length is 12.1 mm.

We contend that the eventual stability of nomenclature is better served by accepting the priority of *ladon* over *pseudargiolus* than by ignoring the Cramerian name. Whatever name is eventually accepted, it will probably take a decision of the I. C. Z. N., especially if the Boisduval and Leconte name is to be accorded legitimacy. Such a decision would end the *ladon-pseudargiolus* argument that seems to surface about every fifty years. In any event, merely ignoring *ladon* can no longer be done with impunity.

The Nearctic subspecies of *ladon* are precisely those cited in most references (dos Passos, 1964) for *argiolus*, the only exception being the replacement of *pseudargiolus* by *ladon* and the subspecies being allied with *ladon*. The nomenclature cannot be too upset by this change. An even more radical taxonomy of the Nearctic *argiolus*-group utilizes the Amadon-Short (1976) scheme, wherein the American species and subspecies would be (without synonymy):

Celastrina [*argiolus*] *ladon* (Cramer, 1780)
    a. *Celastrina ladon lucia* (W. Kirby, 1837)
    b. *Celastrina ladon ladon* (Cramer, 1780)
    c. *Celastrina ladon argentata* (Fletcher, 1903)
    d. *Celastrina ladon nigrescens* (Fletcher, 1903)
    e. *Celastrina ladon sidara* (Clench, 1944)
    f. *Celastrina ladon echo* (W. H. Edwards, 1864)
    g. *Celastrina* (*gozora*) *cinerea* (W. H. Edwards, 1883)
    h. *Celastrina* (*ladon*) *gozora* (Boisduval, 1870)
Celastrina [*argiolus*] *ebenina* Clench, 1972

Note that these combinations include superspecies, species, mega-subspecies and subspecies and show relationships somewhat better than conventional synonymy. Parenthetically, we hasten to add that we do not expect this scheme to be adopted generally for some time.[2]

ACKNOWLEDGMENTS

We wish to thank especially our wives and colleagues, Dr. Mary H. Clench and Mrs. Jacqueline Y. Miller, for their unstinting support and encouragement through the project. Mrs. Miller also read and commented upon the manuscript, as did Dr. John C. Downey and Mr. A. C. Allyn. To all we owe a great debt of thanks.

Thanks are also due various foreign and domestic colleagues for their assistance in checking references, looking for specimens and for advice on the procedure. Special among these individuals are Dr. Rienk de Jong (Rijksmuseum, Leiden, Netherlands), Mr. R. I. Vane-Wright (British Museum (Natural History), London, England) and Col. John Eliot (Taunton, Somerset, England) for discussions and special help not otherwise mentioned here.

LITERATURE CITED

AMADON, D. & L. R. SHORT. 1976. Treatment of subspecies approaching species status. Syst. Zool. 25: 161–167.

BARNES, W. & J. McDUNNOUGH. 1917. Check list of the Lepidoptera of boreal America. Herald Press, Decatur, Ill. v–viii + 392 p.

BELL, E. L. 1941. On *Lerodea telata* Herrich-Schaeffer and *tyrtaeus* Plotz (Lepidoptera: Hesperiidae). Entomol. News 52: 183–185.

BOISDUVAL, J. A. B. D. 1870. Considerations sur des Lépidoptères envoyes du Guatemala á M. de l'Orza. Oberthür et fils, Rennes, France. 100 p.

——— & J. LECONTE. [1833]. Histoire générale et iconographie des Lépidoptères et des chenilles de l'Amerique septentrionale. Roret, Paris. 228 p. + 78 pl.

BROWN, F. M. & W. D. FIELD. 1970. *Papilio hyllus* Cramer 1776, vs. *Polyommatus thoe* Guerin-Meneville 1831, and the "50-year rule" (Lep.: Lycaenidae). J. New York Entomol. Soc. 78: 175–184.

CLENCH, H. K. 1972. *Celastrina ebenina*, a new species of Lycaenidae (Lepidoptera) from the eastern United States. Ann. Carnagie Mus. 44: 33–44.

CRAMER, P. [1775]–[1780]. De Uitlandsche Kapellen voorkomende in de drie Waerelddeelen Asia, Africa en America [also an equivalent French title]. S. J. Baalde, Amsteldam. Vols. 1–3 only.

DICKSON, C. G. (with D. M. KROON) (ed.). 1878. Pennington's butterflies of southern Africa. Ad. Donker (Pty.) Ltd., Johannesburg. 669 p., 198 pl., 1 map.

DRAUDT, M. 1921. *In* A. Seitz (ed.), Grossschmetterlinge der Erde 5: 818.

——— 1924. Ibid.: 932.

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[2] When this paper was in final preparation, I received a note from Col. Eliot concerning *ladon*. In part, it read as follows: "Since I saw you, I have examined Cramer's original watercolour. It is a very much more life-like representation than the caricature in Pl. 270, Figs. D, E. As a result, I now have no hesitation in identifying *ladon* with *pseudargiolus* and *violacea*, and I shall now use *ladon* in Kawazoe's & my paper for the *argiolus* subsp. from eastern USA."

The assignment of *ladon* to *argiolus* is still a matter of some disagreement, except with the latter being considered a superspecies, as is discussed in the present paper. [LDM]

DYAR, H. G. 1902. A list of North American Lepidoptera and key to the literature of this order of insects. Govt. Printing Off., Washington. v–xix + 723 p.

EVANS, W. H. 1949. A catalogue of the Hesperiidae from Europe, Asia and Australia in the British Museum (Natural History). Trustees British Mus., London. v–xix + 502 p., 53 pl.

—— 1953. A catalogue of the American Hesperiidae in the British Museum (Natural History). Part 3, Pyrginae, section 2. Trustees British Mus., London. v–viii + 246 p., 53 pl.

—— Ibid. Part 4, Hesperiinae and Megathyminae. Trustees British Mus., London. v + 499 p.; pl. 54–88.

FABRICIUS, J. C. 1775. Systema entomologiae sistens Insectorum . . . Libr. Kortii, Flensburgh and Leipzig. xxx + 832 p.

—— 1776. Genera insectorum . . . Bartsch, Chilonii. 310 p.

—— 1793. Entomologica Syetematica . . . vol. 3. Proft, Copenhagen. iv + 487 p.

GUÉRIN-MÉNÉVILLE, F. E. [1831]. In G. Cuvier, Iconographie du regne. Animal 10: 576 p., 450 pl.

HÜBNER, J. [1827–1831]. Zuträge zur Sammlung exotischer Schmetterlinge, vol. 3, p. 28 only.

HUMPHREYS, H. N. & J. O. WESTWOOD. 1841. British butterflies and their transformations. William Smith, London. xii + 130 + [10] p. 42 pl.

I. C. Z. N. = International Commission for Zoological Nomenclature and its successor the International Trust for Zoological Nomenclature, various dates. Decisions, Official Lists and Indices and International Code of Zoological Nomenclature.

KIRBY, W. 1837. Insects, in J. Richardson, Fauna boreali-Americana . . . 4. Longman, London. xxxix + 325 p.

DE L'ORZA, P. 1869. Les Lepidopteres japonais . . . Oberthür et fils, Rennes. 49 p.

LINNAEUS, C. 1758. Systema Naturae . . . ed. 10. L. Salvii, Holmiae. 2 vols.

—— 1764. Museum . . . Ludovicae Ulricae . . . Priv. publ., Stockholm. i–vi + 720 p.

—— 1767. Systema Naturae . . . ed. 12. Priv. publ., Stockholm. 744–900.

MÉNÉTRIÉS, E. 1857. Enumeratio corporum animalium Musei imperialis academiae scientarum Petropolitanae. Classis Insectorum, Ordo Lepidopterorum. St. Petersburg [Leningrad]. 3 vols.

MILLER, L. D. & F. M. BROWN. 1979. Studies in the Lycaeninae (Lycaenidae). 4. The higher classification of the American Coppers. Bull. Allyn Mus. (51): 30 p.

OPLER, P. A. 1975. Lycaeninae. In W. H. Howe (ed.), Butterflies of North America. Doubleday and Co., Garden City, New York. 309–316.

SCUDDER, S. H. 1863. A list of the butterflies of New England . . . Proc. Essex Inst. 3: 161–179.

—— 1889. The butterflies of the eastern United States and Canada with special reference to New England. Priv. Publ., Cambridge, Massachuetts. 3 vols.

ANNOTATED LIST OF BUTTERFLIES OF
SAN SALVADOR ISLAND, BAHAMAS

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ABSTRACT. Collection records for 41 species of butterflies from San Salvador Island, the Bahamas, are reported. These include the first Bahamian records for *Eunica tatila tatilista, Eunica monima,* and *Hypolimnas misippus.* Some notes on ecology of certain species are also included.

San Salvador Island lies along the easternmost flank of the Bahamas, approximately 600 km SE of the coast of Florida and 320 km from Cuba. This island is 21 km in length (N–S) and 8 km wide. Its vegetation has been described by Smith (1975) as subtropical scrub.

Several individuals and groups have collected butterflies on the island, including Worthington in 1909, the Armour Expedition in the 1930's, the John R. Hayes family in 1974 and the Van Voast Expedition of the American Museum of Natural History in 1953 (Rindge, 1955). As a result of these collections, a total of 20 species of butterflies were reported from the island.

Since December, 1975, students from Hartwick College have been collecting insects on the island yearly. Their collections bring the total number of butterfly species reported from the island to 41, and the first Bahamian records for three species, *Eunica tatila, Eunica monima,* and *Hypolimnas misippus,* are among these.

This paper lists records for all butterflies collected on San Salvador. The species are arranged by family and species in the order used by Riley (1975). Older collection records are followed by abbreviations for the museums in which the specimens are deposited. Abbreviations are as follows: CM, Carnegie Museum of Natural History; MCZ, Museum of Comparative Zoology; AMNH, American Museum of Natural History.

Collecting Localities and Common Species

Smith (1975) distinguished several vegetation zones on the island, each characterized by soil type and vegetation assemblage (Smith,
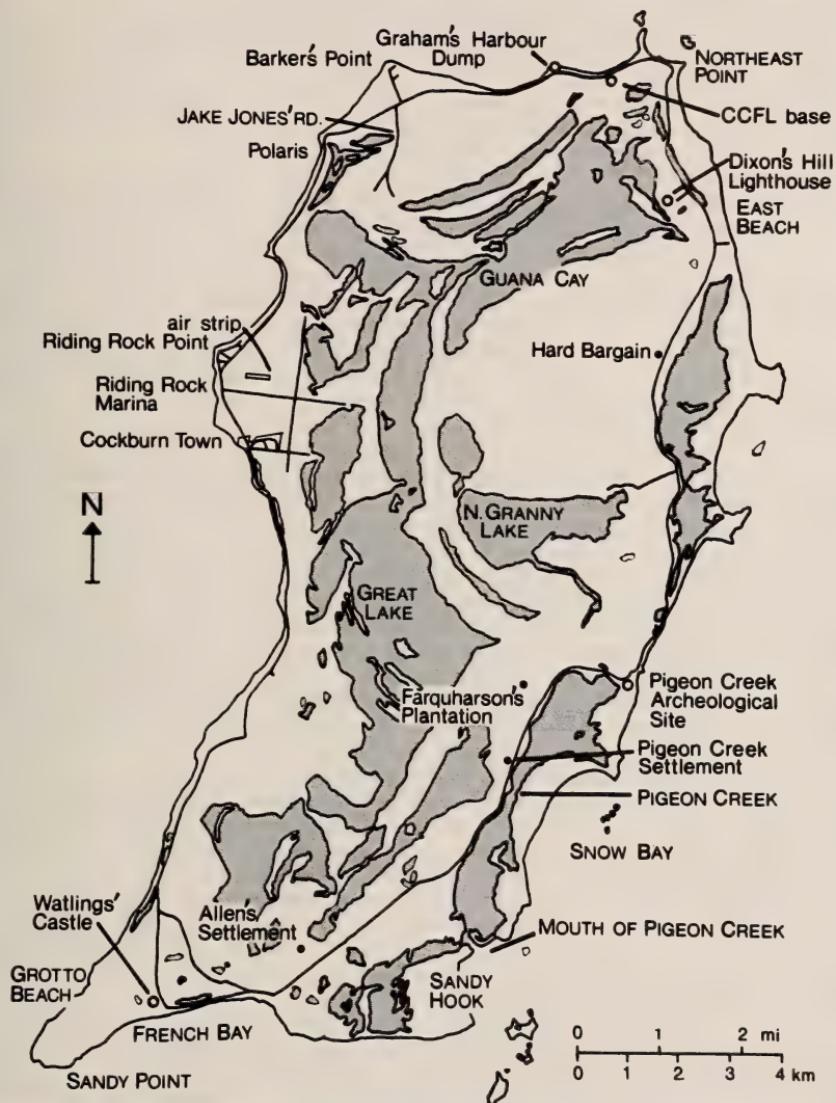
Fig. 1. Map of San Salvador Island, Bahamas, showing collection localities.

unpubl.). The following descriptions of our collecting localities, in-dicated in Fig. 1, utilize his terms for the vegetation types.

1. College Center of the Finger Lakes Base (CCFL). This old naval base at Graham's Harbor is now operated as a field station by the College Center of the Finger Lakes.

It serves as our headquarters during collecting trips. The lawns on the base are mowed, and ornamentals such as oleander, frangipani, and hibiscus have been planted. A few common butterflies on the base include *Anartia jatrophe guantanamo*, *Dryas iulia carteri*, *Eurema elathea*, and *Eurema lisa sulphurina*.

2. Graham's Harbor Dump. A sandy road runs from the highway through an area of disturbed coastal thicket to the open dump area on the coast. The most common plants along the road are *Croton discolor* Willd., *Cassia bicapsularis* L., *Corchorus hirsuta* L., and *Lantana involucrata* L. (Salbert & Elliott, 1979). Among the common butterflies along the dump road are *Agraulis vanillae*, *Battus polydamas*, *Phoebis agarithe antillia*, and *Eurema chamberlaini chamberlaini*.

3. Jake Jones' Road. This road runs about 3.2 km into the island's interior, from an area of coastal thicket at its intersection with the highway, through coppice. The trail ends in an open area, grazed by wild cattle. Milkweed, *Asclepias curassavica* L., is common, and individuals of *Danaus plexippus megalippe* are usually seen. Along the trail in areas of coppice, poisonwood, *Metopium toxiferum* (L.) Krug. & Urb., is one of the most common trees. In the more open areas, Christmas bush, *Cassia bicapsularis* L., is common, as is low-growing life plant, *Kallanchoe pinnata* (Lem.) Pers. This trail shows a great diversity of Lepidoptera, undoubtedly because of the ecological diversity along it. Several species of *Eurema* are found: *E. chamberlaini*, *E. elathea*, *E. messalina*, and *E. dina helios*. Other species occurring here include *Papilio andraemon bonhotei* and *Junonia genoveva*.

4. Near Polaris. This is an area of the vegetation type that Smith (ibid.) calls *Coccothrinax* scrub. The soil here is light-colored sand, and the vegetation is characterized by shrubs and palms. Epiphytic species of *Tillansia* and *Encyclia* are common. *Junonia genoveva* is a characteristic species in this locality, and during our studies *Ascia monuste eubotea* was collected almost exclusively there.

5. Cockburntown and Riding Rock. Cockburntown is the island's largest town. There are many private homes with ornamentals planted here. The Riding Rock Inn, the major tourist hotel, is about 1.6 km N of the town near the airstrip. The Riding Rock Marina lies midway between the inn and the town. Earlier butterfly collectors concentrated their efforts in this area of the island, but we have done little collecting there.

6. Near French Bay. This is an area at the south end of the island, which Smith (ibid.) designated rocky coppice because of the limestone substrate. There are many deep pits in the limestone, and most of the individuals of *Marpesia eleuchea bahamensis* seen or collected were flushed from these pits.

7. Sandy Hook. This is a peninsula at the southeastern end of the island, bounded on the south and east by Snow Bay and on the north by the mouth of Pigeon Creek. Smith calls its vegetation *Coccothrinax* scrub because of its white sandy soil and low-growing vegetation. *Euptoieta hegesia hegesia* is especially common here.

8. Trail to North Granny Lake. This trail runs into the interior from the highway on the island's east side. About .8 km inward, there is a small tidal pond where we concentrated our collecting efforts. The trail to this point is being invaded by haulback, *Mimosa bahamensis* Benth. Characteristic butterflies here include *Calisto herophile apollinis* and *Hylephila phyleus phyleus*.

9. Trail to East Beach. This trail runs less than .8 km through blacklands to the *Uniola* strand which adjoins the beach. The vegetation is characterized by shrubs, especially species of *Croton*. Several species of lycaenids are common here including *Strymon acis armouri*, *Electrostrymon angelia dowi*, and *Leptotes cassius theonus*.

10. Guana Cay. This area is located on the shore of Great Lake, one of the brackish lakes in the island's interior. Along the lake's shore there is an open mangrove area; this is surrounded by coppice. Two butterfly species characteristic of the mangroves are *Anaea verticordia* and *Lucinia sida albomaculata*. Within the coppice *Eunica tatila tatilista* occurs.

Collecting Results

Numbers in parentheses indicate specimens collected.

DANAIDAE

Danaus plexippus megalippe Hübner, 1824. 24 Feb. 1909, nfd[2] (CM); 30 Nov. 1975; 1 Dec. 1975, 25 Nov. 1976 (3), 24 Nov. 1977, 29 Nov. 1977, end of Jake Jones' Rd; 1977, nfd. Adults were usually associated with the milkweeds at the end of Jake Jones' Road.

Danaus gilippus berenice Cramer, 1779. 17 Feb. 1933, nfd (CM).

SATYRIDAE

Calisto herophile apollinis Bates, 1934. 9 Dec. 1977, trail to N. Granny Lake. The only specimen was collected in an area of thick coppice where haulback predominated.

NYMPHALIDAE

Anaea verticordia Hübner, 1824. 21 July 1974, NE Point (CM); 30 Nov. 1975; 1977, nfd (8); 25 Nov. 1976, Jake Jones' Rd (2); 12 Dec. 1976, Grotto Beach; 30 Nov. 1977, Sandy Hook; 1 Dec. 1977, Jake Jones' Rd; 2 Dec. 1977, Guana Cay; 29 Nov. 1978, Farquharson's Plantation; 29 Nov. 1978, W Pigeon Creek; 5 Dec. 1978, trail to E Beach; 14 Dec. 1978, Graham's Harbor Dump. This species was collected at several different localities. Its behavior is best observed in the mangroves at Guana Cay where individuals alight upside down near the base of limbs.

Marpesia eleuchea bahamensis Munroe, 1971. 25 Nov. 1976, Jake Jones' Rd; 5 Dec. 1977, nr. French Bay (2). This species is rather rare, but we have seen it several times in the rocky coppice near French Bay, where individuals have been flushed from limestone pits.

Lucinia sida albomaculata Rindge, 1955. 2 Dec. 1977, Guana Cay (2); 2 Dec. 1977, Graham's Harbor Dump; 23 Nov. 1978, Jake Jones' Rd; 6 Dec. 1978, Guana Cay. While we have collected the species elsewhere on the island, it is most commonly associated with the mangroves at Guana Cay.

Eunica tatila tatilista Kay, 1926. 2 Dec. 1977, 6 Dec. 1978, Guana Cay. This is the first Bahamian record of this species. Although a coloring book about Bahamian butterflies (Anon., 1974) listed it from Andros, Clench (1977) did not collect it there. On San Salvador this species was restricted to coppice in the interior of the island. We collected it only on our expeditions to Guana Cay.

Eunica monima Cramer, 1782. 22 Nov. 1978, intersection Jake Jones' Rd and highway. This species, like the preceding, has never before been reported from the Bahamas. Riley (1975) reported it from Cuba, Haiti, the Dominican Republic, Jamaica and Puerto Rico, and mentioned its migratory habits. It remains to be seen whether this specimen represents an isolated migratory individual, or whether the species has established a population on the island.

Hypolimnas misippus misippus Linn., 1764. 17 Nov. 1978, road W of CCFL Base; 9 Dec. 1978, Pigeon Creek Settlement. This is also a new species record for the Bahamas. Two females were collected at opposite sides of the island, and one of us (D. R.) also saw a male, which was not collected. These findings suggest that the species is breeding on San Salvador.

Junonia coenia Hübner, 1822. 30 Nov. 1978, Allen's settlement.

Junonia genoveva Cramer 1780. 24 March 1909, nfd (CM); 20 Nov. 1975, nfd; 26 Nov. 1976, nr. Polaris; 15 Dec. 1976, 1 Dec. 1977, Jake Jones' Rd.

Anartia jatrophe guantanamo Munroe, 1942. 13 March 1909, nfd (CM); 18 March 1953, nr. Cockburntown (Rindge, 1955) (AMNH); 22 July 1974, Riding Rock Marina (2) (CM); 21 Nov. 1977, 21 Nov. 1978, CCFL Base; 21 Nov. 1977, 3 Dec. 1978, Graham's Harbor Dump; 24 Nov. 1977, 1 Dec. 1977 (2), 4 Dec. 1978, Jake Jones' Rd; 5 Dec. 1978, trail to E Beach. This species is especially common in developed areas, such as the CCFL Base and the Cockburntown area.

Vanessa cardui Linn., 1758. 14 Dec. 1976, Watlings' Castle; 22 Nov. 1978, Graham's Harbor Dump. According to Riley (1975) isolated migratory individuals are occasionally collected in the West Indies. This seems to be the case for San Salvador.

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[2] nfd = no further data available.

Euptoieta hegesia hegesia Cramer, 1779. 11 March 1909, Cockburntown; 13–27 March 1909, nfd (13) (CM); 18 March 1953, nr. Cockburntown (AMNH) (Rindge, 1955); 21 July 1974, Riding Rock Marina (CM); 22 Nov. 1976, 21 Nov. 1977, 21 Nov. 1978, 4 Dec. 1978, CCFL Base; 25 Nov.–16 Dec. 1976, 24 Nov. 1977; 23 Nov. 1978, Jake Jones' Rd; 30 Nov. 1976 (2), 6 Dec. 1978, Sandy Hook; 14 Dec. 1976, Watlings' Castle; 23 Nov. 1977, Graham's Harbor Dump (2); 29 Nov. 1978, W of Pigeon Creek. This species is among the most common on the island.

HELICONIIDAE

Dryas iulia carteri Riley, 1926. 30 Nov. 1975, nfd; 23 Nov. 1976, 22 Nov. 1978, CCFL Base; 26 Nov. 1976, nr. Polaris; 13 Dec. 1976, 1 Dec. 1977, 1 Dec. 1978 (2), Jake Jones' Rd. This butterfly is common in developed areas of the island. Individuals are frequently near buildings on the CCFL base.

Agraulis vanillae insularis Maynard, 1889. 11–17 March 1909, nfd or Cockburntown (series) (CM); 1939, nfd (MCZ); 18 March 1953, nr. Cockburntown (AMNH) (Rindge, 1955); 21–22 July 1974, Riding Rock Marina (6) (CM); 21 July 1974, NE Point (CM); 21–25 Nov. 1975, nfd; 22 Nov. 1976, 21 Nov. 1977 (3), CCFL Base; 15 Dec. 1976, 24 Nov.–2 Dec. 1977 (2), 4 Dec. 1978, Jake Jones' Rd; 28 Nov. 1977, nr. Polaris; 1 Dec. 1978, nfd; 6 Dec. 1978, Guana Cay. This species, like *Euptoieta hegesia hegesia*, is one of the most common on the island.

LYCAENIDAE

Strymon martialis Herrich-Schäffer, 1864. 18 March 1953, nr. Cockburntown (AMNH) (Rindge, 1955).

Strymon acis armouri Clench, 1943. 22 Nov. 1976, CCFL Base; 14 Dec. 1978, Jake Jones' Rd; 28 Nov. 1977, nr. Polaris; 4–14 Dec. 1978 (2), Graham's Harbor Dump; 5 Dec. 1978, trail to E Beach; 6 Dec. 1978, Guana Cay.

Strymon columella cybira Hewitson, 1874. 17 March 1909, nfd (CM); 18 March 1953, nr. Cockburntown (AMNH) (Rindge, 1955); 29 Nov. 1978, nr. Pigeon Creek; Nov–Dec. 1978, nfd.

Electrostrymon angelia dowi Clench, 1941. 5 Dec. 1978, trail to E Beach.

Leptotes cassius theonus Lucas 1857. 11 March 1909, Cockburntown (CM); 13 March 1909, nfd (CM); 17 Feb. 1933 (MCZ) (Clench, 1943); 18 March 1953, Cockburntown (AMNH) (Rindge, 1955); 4 Dec. 1975, nfd; 22 Nov. 1977, Graham's Harbor Dump; 23 Nov. 1978, Barker's Point; 27 Nov. 1978, CCFL Base; 29 Nov. 1978, W Pigeon Creek (4); 5 Dec. 1978, trail to E Beach (10). This is the most common species of lycaenid on San Salvador. Individuals are very commonly seen on vegetation, especially *Croton* along trails and roads on the island.

Hemiargus thomasi Clench, 1941. 13 March 1909, nfd (CM).

PIERIDAE

Ascia monuste eubotea Latreille, 1819. 11 March 1909, Cockburntown (CM), 13–20 March 1909, nfd (2) (CM); 17 Feb. 1933, nfd (7) (MCZ); 18 March 1953, Cockburntown (AMNH) (Rindge, 1955); 21 July 1974, NE Point (5) (CM); 15–26 Nov. 1976 (2), 28 Nov. 1977 (1), nr. Polaris; 15 Nov. 1976, Jake Jones' Rd. While this species was collected frequently from the island in the past, most of the specimens we collected were from the area of *Coccothrinax* scrub near Polaris.

Eurema chamberlaini chamberlaini Butler, 1898. 17 Feb. 1933, nfd (2) (MCZ); 21 July 1974, NE Point (5) (CM); 22 Nov. 1976, 23 Nov. 1978, CCFL Base; 24 Nov. 1976, 13 Dec. 1976, 24 Nov.–1 Dec. 1977 (2); 24 Nov. 1978, Jake Jones' Rd; 2 Dec. 1977, Guana Cay; 21 Nov.–14 Dec. 1978, Graham's Harbor Dump (2); 5 Dec. 1978, trail to E Beach (2).

Eurema elathea elathea Cramer, 1775. 2 Dec. 1976, 27 Nov. 1978, CCFL Base; 16 Dec. 1977, 1 Dec. 1978, Jake Jones' Rd.

Eurema lisa sulphurina Poey 1853. 22 Nov. 1976, CCFL Base.

Eurema messalina blakei Maynard 1891. 13 Dec. 1976, 1 Dec. 1977 (2) Jake Jones' Rd; 14 Dec. 1976, Watlings' Castle; 29 Nov. 1978, Pigeon Creek Archeological Site (2); 6 Dec. 1978, Guana Cay.

Eurema dina helios Bates, 1934. 24 Nov. 1976, 1 Dec. 1977, Jake Jones' Rd. *Eurema chamberlaini* was the most widely distributed of the species of *Eurema* on the island. It occurred in disturbed areas such as the CCFL Base and the dump as well as in other habitats such as coppice, coastal thicket and blacklands. *E. messalina blakei*, on the other hand, was restricted to coppice areas. The other species of *Eurema* were collected rarely, and it is impossible to generalize about their distribution patterns.

Kricogonia lyside Godart, 1819. 17 Feb. 1933, nfd (MCZ): 23 Nov. 1976 26 Nov.–1 Dec. 1978 (2), CCFL Base; 26 Nov. 1976, nr. Polaris; 5 Dec. 1976, 1 Dec. 1977, 22 Nov. 1978, Jake Jones' Rd; 22 Nov. 1977 (2), 4 Dec. 1978, Graham's Harbor Dump.

Phoebis agarithe antillia Brown, 1919. 13 March 1909, nfd (CM); 17 Feb. 1933, nfd (MCZ): 21 July, 1974, NE Point (CM); 21 July, 1974, Riding Rock Marina (3) (CM); 20–26 Nov. 1975, nfd (4); 22–23 Nov. 1976 (2), 21 Nov. 1978, CCFL Base; 2 Dec. 1976, Watlings' Castle; 1 Dec. 1977, Jake Jones' Rd; 21–23 Nov. 1978, Graham's Harbor Dump (3); 7 Dec. 1978, Sandy Hook. This species is more frequently collected in disturbed areas than is *Phoebis sennae*, but it is also found in coppice, and in *Coccothrinax* scrub. It is often seen along the highway.

Phoebis sennae sennae Linn., 1758. 13–25 March 1909, nfd (2) (CM); 17 Feb. 1933, nfd (3) (MCZ); 26 Nov. 1976, nr. Polaris; 13 Dec. 1976 (3), 24 Nov.–1 Dec. 1977 (3), 22 Nov. 1978 (1), Jake Jones' Rd; 14 Dec. 1976 (4), Watlings' Castle; 5 Dec. 1978, trail to E Beach. This species is seen less frequently in developed areas than *P. agarithe*, and has been collected most frequently in coppice. It also has been collected in *Coccothrinax* scrub and in the blacklands. The species apparently is migratory, and Williams et al. (1942) reported an 1889 account of this species passing over San Salvador in migration.

PAPILIONIDAE

Battus polydamas lucayus Rothschild & Jordan, 1906. 20 Nov.–2 Dec. 1975, nfd (2); 23 Nov. 1976, 29 Nov.–3 Dec. 1977, CCFL Base; 14 Dec. 1976, Watlings' Castle; 22 Nov. 1977, Graham's Harbor Dump; nfd (4).

Papilio andraemon bonhotei Sharpe, 1900. 21–30 Nov. 1975, nfd (3); 2 Dec. 1976, Watlings' Castle.

HESPERIIDAE

Epargyreus zestos zestos Geyer, 1932. 25 Nov. 1976, 24 Nov. 1977, 23 Nov. 1978, Jake Jones' Rd; 30 Nov. 1976, 1 Dec. 1977, Sandy Hook; 5 Dec. 1977, Sandy Point; 23 Nov. 1978, CCFL Base; 26 Nov. 1978, Farquharson's Plantation; 29 Nov. 1978, W Pigeon Creek; 5 Dec. 1978, nr. E Beach; 28 Nov. 1977, nr. Polaris.

Polygonus leo savignyi Latreille, 1824. 1 Dec. 1977 (2), 1 Dec. 1978, Jake Jones' Rd.

Urbanus proteus domingo Scudder, 1872. 3–17 March 1909, nfd (2) (CM); 17 Feb. 1933, nfd (2) (MCZ); 21 Nov. 1975, nfd; 24 Nov.–13 Dec. 1976 (5), 25 Nov.–1 Dec. 1977 (2), 1 Dec. 1978, Jake Jones' Rd; 14 Dec. 1976, Watlings' Castle (2); 25 Nov. 1977, 24 Nov. 1978 (2), nr. Polaris; 23–24 Nov. 1978, CCFL Base.

Ephryiades brunnea brunnea Herrich-Schäffer, 1864. 11 March 1909, Cockburntown; 3 March 1909, nfd (CM).

Hylephila phyleus phyleus Drury. 11 March 1909, Cockburntown; 3–24 March 1909, nfd (CM); 18 March 1953, nr. Cockburntown (AMNH) (Rindge, 1955); 14 Dec. 1976, Watlings' Castle; 15 Dec. 1976, nr. Polaris; 2 Dec. 1977, Graham's Harbor Dump; 8 Dec. 1977, 5 Dec. 1978, trail to N Granny Lake.

Wallengrenia misera Lucas, 1857. 3 March 1909, nfd (CM); 18 March 1953, nr. Cockburntown (AMNH) (Rindge, 1955).

Euphyes cornelius cornelius Latreille. 15 Dec. 1976, Jake Jones' Rd.

ACKNOWLEDGMENTS

We appreciate the assistance of Dr. R. R. Smith, Dept. of Biology, Hartwick College, for helping us with plant identifications, and for

helpful criticism of our descriptions of collecting localities, and for allowing us to quote from his unpublished manuscript.

The studies on San Salvador were conducted through programs of the College Center of the Finger Lakes. We thank Dr. Donald Gerace and Mrs. Kathy Gerace for their assistance during our stays on the island.

The map of San Salvador was drawn by Nancy Perkins, Carnegie Museum of Natural History.

LITERATURE CITED

ANONYMOUS. 1974. Bahama Butterflies and Moths Coloring Book. Etienne Dupuch, Jr., Nassau. 48 p.

CLENCH, H. K. 1943. The Lycaenidae of the Bahama Islands (Lepidoptera: Rhopalocera). Psyche 49: 52–60.

——— 1977. A list of the butterflies of Andros, Bahamas. Ann. Carnegie Mus. 46: 173–94.

RILEY, N. D. 1975. A Field Guide to the Butterflies of the West Indies. Collins, London. 224 p.

RINDGE, F. H. 1955. The butterflies of the Van-Voast American Museum of Natural History Expedition to the Bahama Islands, British West Indies. Amer. Mus. Novit. 1715: 1–20.

SALBERT, P. & N. B. ELLIOTT. 1979. Observations on the nesting behavior of *Cerceris watlingensis* (Hymenoptera: Sphecidae, Philanthinae). Ann. Entomol. Soc. Amer. (In press.)

SMITH, R. R. 1975. Ferns of San Salvador Island, the Bahamas. Amer. Fern Journal 65: 63.

——— Unpubl. ms. Vegetation of San Salvador Island, Bahamas.

WILLIAMS, C. B., G. B. COCKBILL, M. E. GIBBS & J. A. DOWNS. 1942. Studies in the migration of Lepidoptera. Trans. R. Entomol. Soc. London. 92: 101–283.

DIANESIA, A NEW GENUS OF RIODINIDAE FROM THE WEST INDIES

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ABSTRACT. *Dianesia,* gen. n., is proposed for the riodinid butterfly originally described as *Charis carteri* Holland. This species, endemic to Cuba and the Bahamas, has long been considered a member of the genus *Apodemia,* from which, however, it is quite distinct. A morphological description and notes on the biology of *D. carteri* are presented.

Holland (1902) described the metalmark *Charis carteri* from specimens collected on New Providence Island, Bahamas. Ten years later, Skinner (1912) described *Mesosemia ramsdeni* from La Yberia, Cuba. Stichel (1911: 290) provisionally transfered *carteri* to the genus *Apodemia* Felder & Felder, an action accepted by subsequent authors (e.g. Bates, 1935; Rindge, 1952; West, 1966; Riley, 1975). We agree with Riley (loc. cit.) in considering *ramsdeni* to be a subspecies of *carteri.* These two taxa represent the only members of the Riodinidae known from the West Indies, and both remained rare in collections. No additional information was gleaned about *carteri* until our fieldwork in the Bahamas during the 1970's. Differences in wing pattern and adult behavior suggested that *carteri* was not congeneric with North and Central American *Apodemia,* and this suspicion was confirmed by comparisons of their appendages and genitalia. We therefore propose the following new genus.

Dianesia Harvey and Clench, new genus

Type species: *Charis carteri* Holland (nominate subspecies).
Description. **Eyes** naked, yellow-green in life. **Palpi** (Fig. 1) slender, appressed to head, not extending beyond frontal vestiture; third segment stubby, one-seventh (male) to one-fifth (female) length of second (in *Apodemia*[2] ratio one-third to almost one-half). **Antennae** slender, seven-tenths length of forewing costa; comprised of 38–39 segments, the terminal 13 forming a weak club. **Forewing** (Fig. 2) and **hindwing** (Fig. 3) not differing consistently in any one character from the range of variation present in *Apodemia*[2]. **Male foreleg** (Fig. 4) very slender; tibia with a single spine (absent in *Apodemia*[2]); tarsus apparently dimerous, equal in length to tibia. **Female**

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[1] Deceased, 1 April 1979.

[2] Species examined: male and female *m. mormo* Felder & Felder, *palmeri* Edwards, *walkeri* Godman & Salvin, *multiplaga* Schaus, and *hypoglauca* Godman & Salvin.
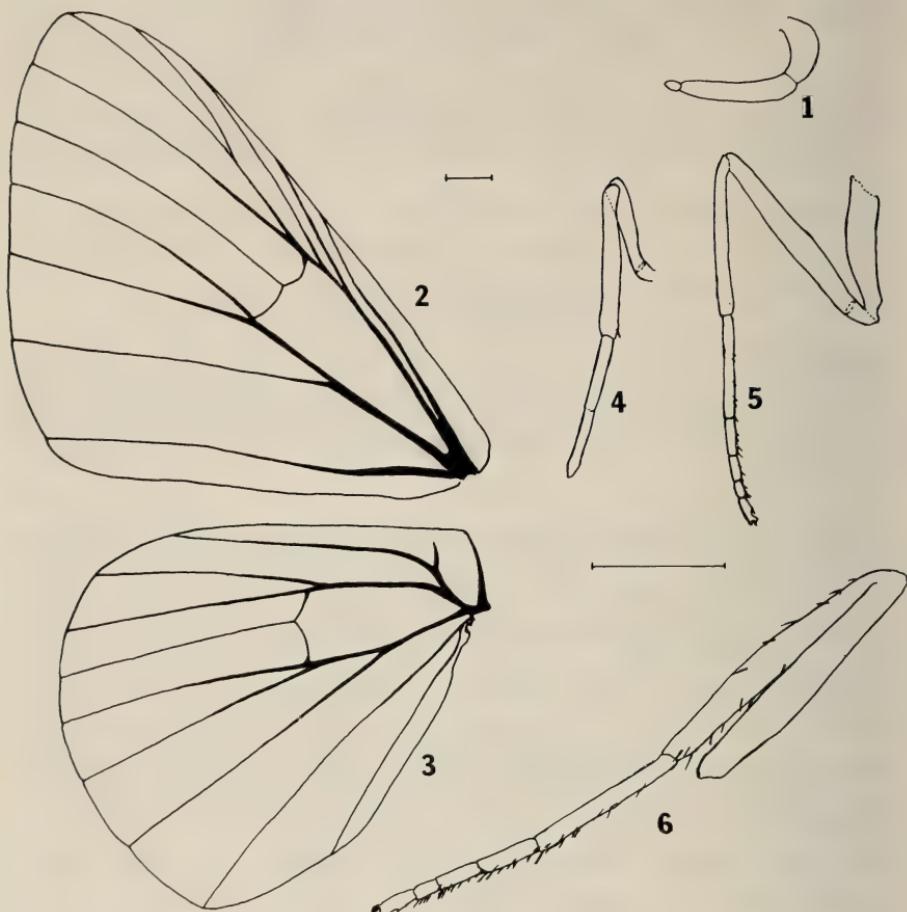
FIGS. 1–6. *Dianesia carteri*. **1,** ♂ palpus; **2,** ♂ forewing venation; **3,** ♂ hindwing venation; **4,** ♂ foreleg; **5,** ♀ foreleg; **6,** ♀ hindleg. Scale lines = 1 mm (upper line for Figs. 2, 3; lower line for Figs. 1, 4–6).

foreleg (Fig. 5) slender, tarsal subsegments with short spines. **Male** and **female mid-** and **hindlegs** lack tibial spurs, although spines are present. Male and female hindleg (Fig. 6) with dorsal spines on tibia (absent in *Apodemia*[2]).

Male genitalia (Figs. 7–9). Uncus weakly lobed, each lobe with a bluntly pointed tooth (absent in *Apodemia*[3]); vinculum in lateral view with an abrupt angle above middle and therefore anteriorly concave (nearly straight or anteriorly convex in *Apodemia*[3]); valvae simple (bifurcate in *Apodemia*[3]), posterior edge lightly sclerotized, becoming membranous towards attachment to vinculum, free ventrally, joined dorsally over the aedeagus by a lightly sclerotized band; saccus reduced, shallowly rounded; aedeagus elongate and slender, slightly curved (bent 45 to 90 degrees in *Apodemia*[3]).

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[1] Species examined include those listed in Footnote 2, in addition to male and female *nais* Edwards, *chisosensis* Freeman and *hepburni* Godman & Salvin (male only).
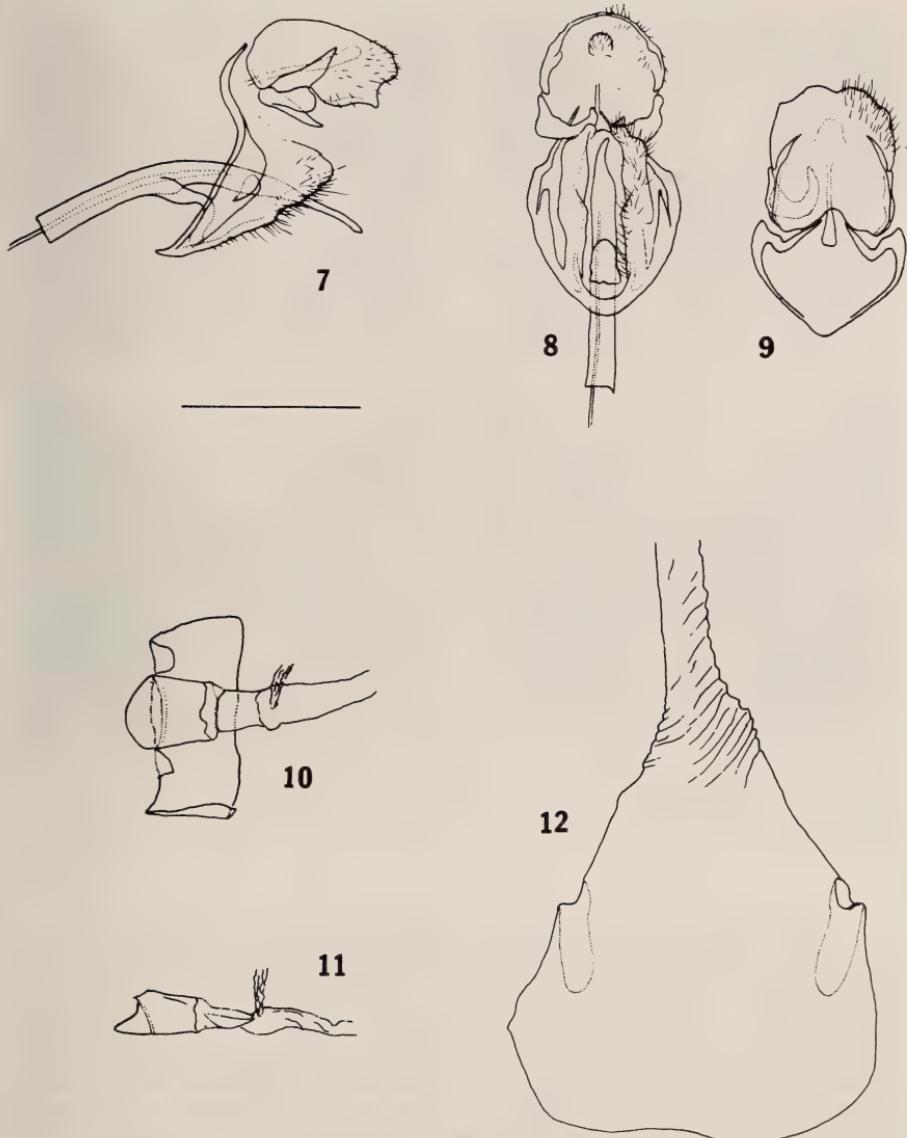
FIGS. 7–12. Genitalia of *Dianesia carteri*. **7,** ♂ lateral view; **8,** ♂ ventral view, setae on right side omitted; **9,** ♂ dorsal view of uncus, tegumen and vinculum; left falx and setae on right side omitted; **10,** ♀ dorsal view—posterior end; **11,** ♀ right lateral view—posterior end; **12,** ♀ corpus bursae. Scale line = 1 mm.

Female genitalia (Figs. 10–12). Eighth sternite punctate, lacking ridges and not sclerotized near ostium bursae (weak ridges present, sclerotized in *Apodemia*[3] except *multiplaga*); ostium bursae dorsoventrally compressed, narrowing towards sclerotized antrum; lamella antevaginalis spatulate and heavily sclerotized, barely covering ostium bursae; lamella postvaginalis weakly sclerotized; ductus seminalis enters dorsally; duc-
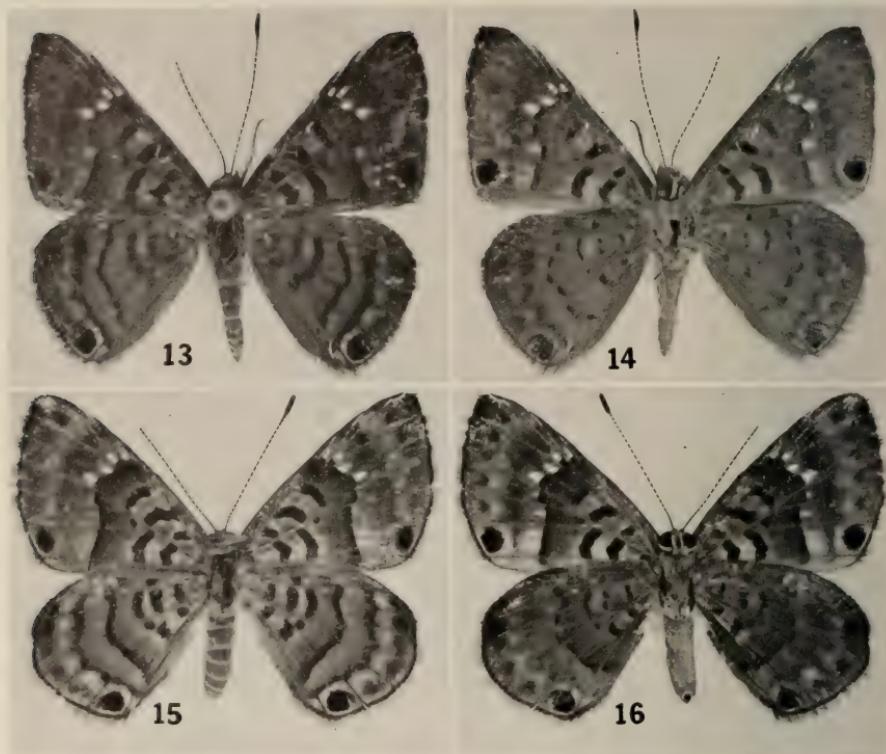
FIGS. 13–16. *Dianesia carteri.* **13,** ♂ dorsal view; **14,** ♂ ventral view; **15,** ♀ dorsal view; **16,** ♀ ventral view.

tus bursae very narrow, very lightly sclerotized, straight (usually heavily sclerotized, with a sharp to slight bend in *Apodemia*[3]), surface punctate, with irregular folds, opening widely into corpus bursae; corpus bursae dorso-ventrally flattened, surface uniformly punctate, with surface folds around junction with ductus bursae.

Relationships. Morphologically, *Dianesia* can be readily separated from Nearctic *Apodemia*[3] (type species: *m. mormo* Felder & Felder) by the characters noted in the description. Without a complete reanalysis of the New World Riodinidae it is impossible to determine the closest affinities of *Dianesia*. Its wing pattern (Figs. 13–16), particularly the tornal eyespot on each wing (above and below), is unusual and resembles that of no other riodinid known to us except, perhaps, for a few vague similarities in some mainland Neotropical species (*Lemonias zygia* Hübner, *Calospila luciana* (Fabricius), *Elaphrotis thelephus* (Cramer)). Genitalic comparisons, however, reveal no close relation to these species. Two South American species attributed to *Apodemia*, *stalachtioides* Butler and *castanea* Prittwitz, were also examined. Differences in genitalia and appendages indicate that they are not congeneric with North and Central American *Apodemia*. Their correct generic assignment is under study.

Natural History. Biological observations on *Dianesia carteri* in the Bahamas have been published elsewhere (Clench, 1967, 1977a, b). During May–June 1978, Harris made additional observations at two N. Andros localities, which, together with the above references, form the basis for the following account.

We have found *Dianesia carteri* in several types of habitat. At West Bay, Little San Salvador, Clench (1977b) found a single female in sparse, open scrub averaging 2 m high. The area had open, sandy ground between the shrubs, which included both fan and Sargent palms, Seagrape (*Coccoloba uvifera*), and a small leafed shrub on which the specimen was found. On both N. and S. Andros, Clench (1976, 1977a) found it flying in stunted, virgin pineland with few scattered shrubs near the coast. On N. Andros, Harvey found *D. carteri* relatively common at Stafford Creek. Most adults seen were perched along a path that ran through a small "coppice," an area of hardwoods with a diverse flora. At Red Bay, a small colony was discovered at a short row of shrubs that bordered the road from the settlement to the public dock. In all instances, *D. carteri* appeared to be very localized, and was usually rare.

Adults perched on the underside of leaves, assuming a characteristic posture: wings almost flat against the leaf, antennae held close together and extended dorsad at a slight angle from the axis of the thorax. This posture resembles that of most Neotropical riodinids, but differs from Nearctic *Apodemia*, which perch on the upperside of leaves or on stems. The perch sites chosen varied from less than 20 cm, to more than 2 m above the ground. At Stafford Creek, certain perch sites appeared to be especially favored by males. When removed from these sites, they were usually replaced by other males in less than 30 min, and certain sites were almost invariably occupied during almost three weeks of intermittent observation.

When visiting flowers, the wings were held outspread. Flowers utilized near Stafford Creek included *Lantana involucrata* (Clench, 1977a), *Bursera simarouba*, and *Coccoloba uvifera*. The latter two also attracted other butterflies, particularly lycaenids. At Red Bay, the flowers of *Cordia bahamensis* were visited, and one female was seen shortly after having been caught at the flowers by a species of *Phymata* (Hemiptera: Phymatidae).

Flight activity of *D. carteri* extended throughout the daylight hours, beginning and ending when most butterflies were inactive. The female from Little San Salvador was taken at 0730 h. At Stafford Creek, males were observed perching as early as 0830 h, and on several occasions were seen visiting *Bursera* flowers around sunset (1930 h).

Despite many hours of field observation, we observed neither courtship nor oviposition, and the larval hostplant and immatures remain unknown. The restriction of *D. carteri* to coastal areas (we have not seen any at distances greater than several hundred meters from open salt water) suggests that the larval hostplant may be similarly restricted.

LITERATURE CITED

BATES, M. 1935. The butterflies of Cuba. Bull. Mus. Comp. Zool. (Harvard) 78: 63–258.

CLENCH, H. K. 1976. In search of rare butterflies. Bahamas Naturalist 2(1): 2–8.

——— 1977a. A list of the butterflies of Andros, Bahamas. Ann. Carnegie Mus. 46: 173–194.

——— 1977b. Butterflies of the Carnegie Museum Bahamas Expedition, 1976. Ann. Carnegie Mus. 46: 265–283.

HOLLAND, W. J. 1902. Two new species of Bahama Lepidoptera. Ann. Carnegie Mus. 1: 486–489.

RILEY, N. D. 1975. A field guide to the butterflies of the West Indies. Demeter Press, New York. 224 p.

RINDGE, F. H. 1952. The butterflies of the Bahama Islands, British West Indies. Amer. Mus. Novit. 1563, 18 p.

STICHEL, H. 1911. Fam. Riodinidae. In Wytsman, P., Genera Insectorum. P. Wytsman, Brussels. 452 p.

WEST, B. K. 1966. Butterflies of New Providence Island, Bahamas. Ent. Rec. 78: 174–179, 206–210.

A RECORD OF *ITAME ABRUPTATA*(GEOMETRIDAE) FROM NEW YORK

During a preliminary survey of the insects associated with ninebark, *Physocarpus opulifolius* (L.) Maxim (Rosaceae), I reared a small lepidopterous larva, collected in a state park in the Finger Lakes Region of New York, to the adult stage. It proved to be the ennomine geometrid *Itame abruptata* (Walker). This is apparently the first record of this species from New York. The identification was made by John G. Franclemont, Cornell University, Ithaca, N.Y. This reared specimen is in the personal collection of Dr. Franclemont, and bears these labels: "N.Y.: Taughannock Falls State Park, US 89 at bridge, 8 mi. N. of Ithaca, Tompkins County, E. R. Hoebeke & M. E. Carter/ EX: *Physocarpus opulifolius/* larva coll. May 16, 1979; pupated by May 27; adult emergence June 7."

Itame abruptata is known to occur from northern Ontario south to western Pennsylvania and west to eastern Minnesota and Missouri (McGuffin 1977, J. Lepid. Soc. 31: 269–274), but appears to be only locally abundant in certain areas of its range. Additional collections of larvae of *I. abruptata* have been made from ninebark in the south-central region of Pennsylvania (Harrisburg and environs) by A. G. Wheeler, Jr. (Pa. Dept. Agric., Harrisburg, Pa.). These reared specimens are in the collections of Cornell University and the Pennsylvania Department of Agriculture. This species is not well represented in North American collections.

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EGGS OF RIODINIDAE

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ABSTRACT. Descriptions and SEM photographs of the eggs of 13 species of Riodinidae are given together with morphological and taxonomic viewpoints of their comparison to eggs of the Lycaenidae.

In our ultrastructural studies of lycaenid eggs (Downey & Allyn, 1980), we have become aware of the lack of comparative details on the egg state of most families of Lepidoptera. Through the kindness of Roy and Connie Kendall, we were able to examine the chorionic structure of riodinids of 13 species representing six genera with the scanning electron microscope (SEM). Most of the life histories of these species have yet to be described. We are unaware of SEM studies on this interesting family. These observations and preliminary notes may be of general interest and may stimulate additional studies. We dedicate this effort to the memory of our friend and colleague, Harry K. Clench, who was enthusiastic about new data on this family and its relationship to the Lycaenidae.

Materials and Methods

All eggs were laid by females (rather than extracted) and were collected and stored in alcohol. Our studies indicate that dried eggs dispatched by cyanide or freezing may be slightly superior to alcohol-stored eggs for SEM examination. The latter are perfectly adequate for SEM work, though they may have lipids and other alcohol extracted materials (see Fig. 19) adhering to the surface, and might best be cleaned with solvent, or sonically cleaned, prior to coating. Freshly collected eggs stored in alcohol also have a tendency to collapse, whereas eggs which have chorions exposed to the air for a few hours seem to retain their shape. Specimens were mounted on JEOL holders by means of double-sided tape edged with a conductive lacquer adhesive prior to coating. They were coated with 40/60 gold-palladium in a Varian V-10 vacuum coater and studied with a JSM-U3 instrument. Results are presented with both descriptions and photographs.

RESULTS

All eggs examined are of the upright type, with the micropyle on the "top" surface opposite the flattened "bottom" surface, which is affixed to the substrate. Although the shapes and sizes of the eggs vary, the micropylar axis (height) is always shorter than the transverse axis (diameter). Most eggs are round when viewed from above, though elevated ribs may disrupt the circumference silhouette. The profile or side view varies from partially flattened, to turban and dome shape in different species. The micropyle is centered on the upper surface and surrounded by a rosette of petal-shaped cells which are outlined by delicate lines. The remaining surface of the chorion is variously sculptured with somewhat defined elevations which appear to impart a species-specific character to the egg. Aeropyles, tiny openings extending into or through the meshwork of the outer chorion, may or may not be visible, and may be located on prominences or (as pores) on relatively flat areas of the chorionic surface. Descriptions of eggs of the individual species follow.

Calephelis rawsoni McAlpine
Figs. 8, 17, 18
d(diameter). 0.62 mm; h(height). 0.28 mm

Egg rounded in dorsal view, though the vertical elevated ridges and protuberances cause irregularities in the circumference shape; in profile flattened on the micropylar surface and angled both at the shoulder, and (less marked) toward the bottom surface; with a marked annulus surrounding the micropylar area, from which 15 ribs radiate outward like spokes in a wheel; the ribs abruptly arch upward as they abut the collar or annulus (Fig. 17) in the manner of a flying buttress; the annulus is honeycombed with small depressions, which have irregular penta- or hexagonal walls, mostly on the upper and the mesial surface; the annulus appears non-porous in *rawsoni,* although many of the same honeycomb depressions in *perditalis* appear open and could serve as aeropyles; the lateral wall of the annulus drops off abruptly and is non-sculptured; the cells (areolae) between the radiating ribs have smooth, unsculptured bottoms, and are more regularly shaped; the second row of cells from the annulus are hexagonal and are set at about 45° from the top and sides of the egg; the ribs are almost perpendicular to the lower chorion; aeropyles are apparent on triangular-shaped prominences (Fig. 18) at the intersections of the ribs of the second row of cells; the third and fourth (bottom) row of cells from the annulus may have sharper prominences at the angle junctures but appear to lack aeropyles.

Micropyle, with four openings, is surrounded by rosette with seven to nine petals depressed into slightly convex surface; area between rosette and annulus smooth, with very faint shallow depressions of the size and appearance of fainter rosette cells.

Eggs from two localities in Texas show a minor degree of variability, particularly in the nature and degree of porosity in the annulus, and in the micropylar depressions. This may be individual rather than geographic variability. Specimens from Kerr Co., Texas, also have a small pore which is slightly larger than the aeropyle openings, which is located between the ribs and the lower chorion at the rib juncture sites beneath the aeropyles.
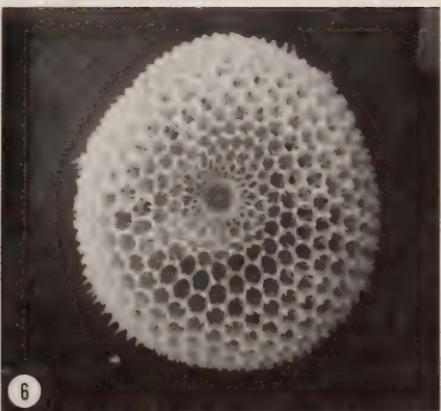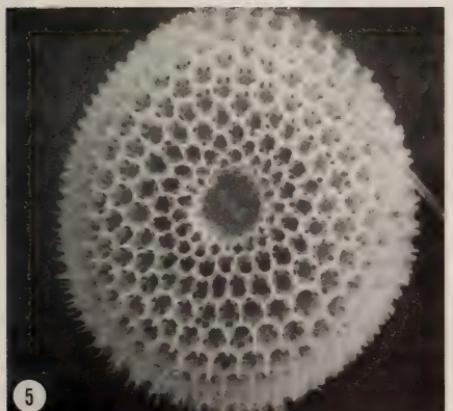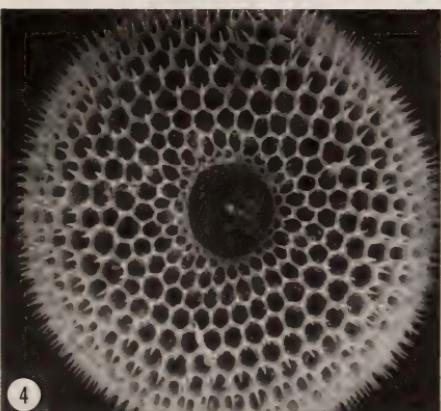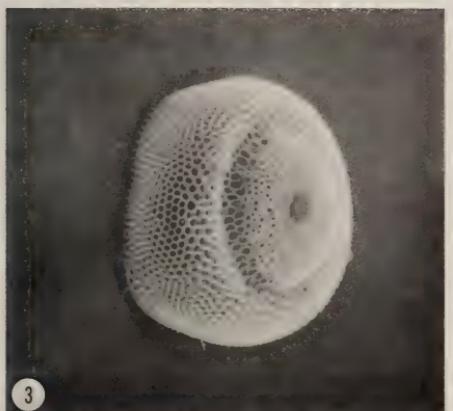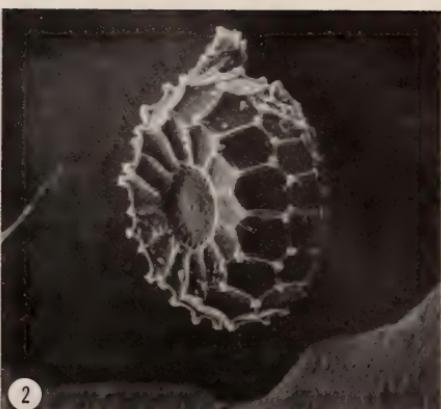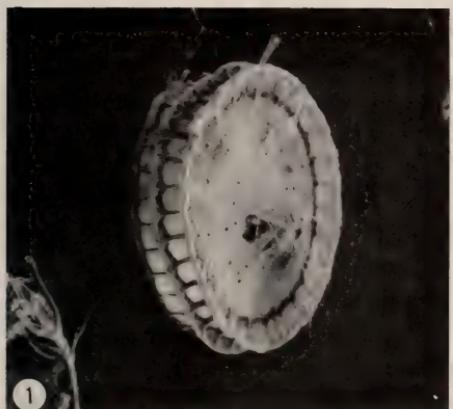
FIGS. 1–6. SEM photos of the eggs of Riodinidae, 60×. **1,** *Lasaia sula penninsularis*; **2,** *Caria ino melicerta*; **3,** *Emesis emisea*; **4,** *E. mandana furor*; **5,** *E. tegula*; **6,** *E. tenedia*. Photographs reduced to 0.58 of original size.

Calephelis perditalis Barnes and McDunnough
Fig. 7
d. 0.60 mm; h. 0.30 mm

External appearance much like *rawsoni* except the collar, or annulus, is slightly smaller in *perditalis*, which also has larger and more open interstices in the honeycomb network; 14 spokes or radii of elevated ribs run from the annulus to the ribs of the second row of cells; 3 openings in micropyle.

In emerging from the egg the larva carves its way out by eating around the annulus, on the outside margin of this honeycomb collar.

Caria ino melicerta Schaus
Fig. 2
d. 0.58 mm; h. 0.30 mm

Chorionic structure similar to *Calephelis rawsoni* and *C. perditalis* except that it is lacking the heavy circum-micropylar collar or annulus; micropylar region slightly depressed, and around the margin of this region on the vertical face (between the micropylar plateau and the level of the surrounding cells) are 25 prominent aeropyles; 13 ribs radiate out from the aeropylar lips to join a chevron-shaped rib outlining the outer margins of the first row of cells; prominent tubercles protrude upward from rib junctions; these hillocks are irregularly shaped masses (like outpourings of lava from a volcanic eruption) and contain very small aeropyles, ¼ the size of the aeropyles in comparable positions in *rawsoni*; second row of cells slightly larger than in *Calephelis*, numbering 13; unique rib structure with either carina on some muri (circumpolar tendency), or central crenulations, running parallel to the rib axis (radiating & vertical rib tendency), giving the ribs the appearance of being composed of more than one parallel element; chorion of cells smooth and structureless.

Four holes in micropyle; micropylar rosette composed of 7 or 8 recessed petals which are very difficult to locate.

Lasaia sula penninsularis Clench
Figs. 1, 20
d. 0.62 mm; h. 0.28 mm

Circular in top view; unique lateral profile having a cup or bowl shape with lateral walls composed of two "rings" of cells with ribs between; lower or third row or ring of cells at about 30° from flattened bottom of egg, so this row is almost hidden in side view; lip of bowl composed of ribs between second row of cells (lateral in position) and first row of cells (dorsal in position) which are lying at 30° above the plane of the upper (micropylar) surface; circular ribs or muri between rows of cells are higher and thicker than vertical or cross ribbing between them, and they may or may not possess one to several carina or raised ridges along their surface; a few small aeropyles at rib junctions, irregularly placed; chorion of cells smooth and unstructured; upper membrane thin and overlaid with very delicate thin ribbing forming irregular hexagonal cells; micropyle with four holes in a small central depression; eight-petal micropylar rosette very difficult to see (Fig. 20) with petals outlined by delicate elevated ribs.

Compare Fig. 20 and 21 which show some of the difficulties of interpreting SEM photographs without the advantage of viewing the object from several directions. The rosette in Fig. 20 has petal outlines which appear to be troughs or depressions; actually they are elevated ribs which become apparent when the figure is viewed upside down. The petals of the rosette in Fig. 21 are outlined by negative depressions, linear indentations in the surface rather than ribs laid on top of the surface.

In Fig. 1, a portion of the thin, delicate upper membrane has been accidentally destroyed by the electron beam, and larval hairs may be noted in the opening. The first instar larva within was not coated, of course, and thus minor "charging" is reflected back through the thin chorionic "floor" of cells in the second and third row of cells,
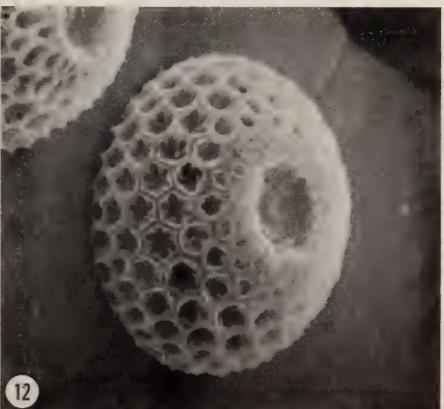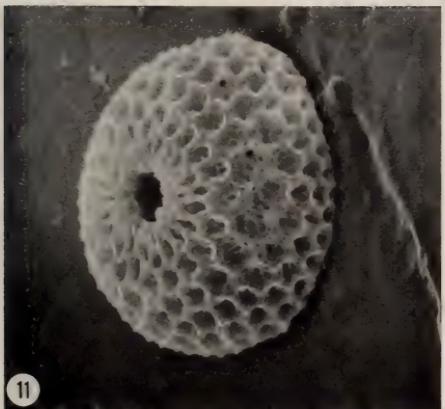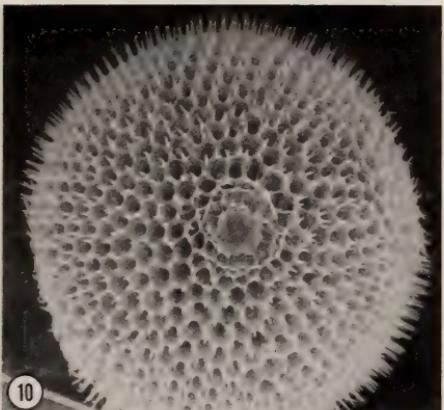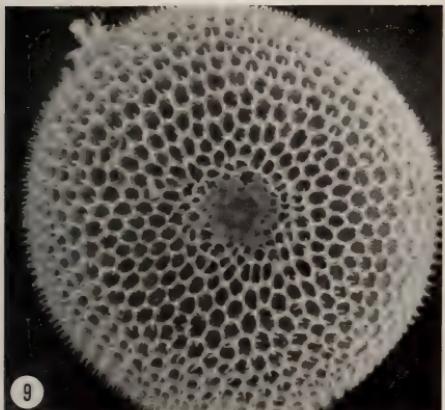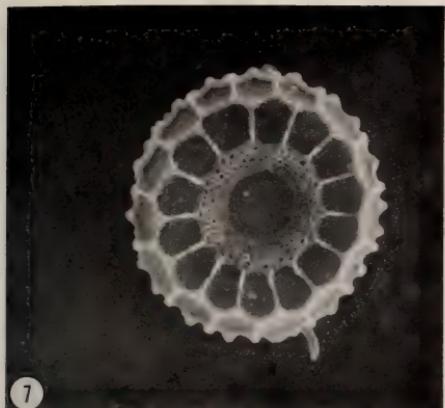
FIGS. 7–12. SEM photos of eggs of Riodinidae, 60×. **7,** *Calephelis perditalis*; **8,** *C. rawsoni*; **9,** *Apodemia mormo mejicana*; **10,** *A. chisosensis*; **11,** *A. palmeri*; **12,** *A. walkeri.* Photographs reduced to 0.58 of original size.

giving the entire egg a flying-saucer appearance (with "lights on" in the windows!). In life, the upper membrane is slightly convex, arching up somewhat from its junction with the first circular row of cells; the arch of the central micropylar "dome" is not as high as the outer edge (ribbing) of the first cell row, so that to the unaided eye the egg may appear strongly shouldered and flat on top.

Emesis emesia (Hewitson)
Figs. 3, 15, 21
d. 0.58 mm; h. 0.30 mm

Egg circular in dorsal view, turban-shaped in side view with the central half of the top surface seemingly depressed downward leaving a circular trough or indentation between apex and shoulder (Fig. 3); all but the micropylar area covered with marked hexagonal honeycomb network, the cells of which are larger (with hexagonal shape distorted) in the trough area; hexagonal cells more regular on sides and toward the bottom of the egg, but rounded on the elevated upper circum-micropylar area; ribs lining the cells in this transitional zone (between micropyle and trough) have dorsal crenulations (Fig. 15) giving them a "frothy" appearance; the roughened froth is arranged in smaller or larger circles atop the ribs, with smaller squares and irregular shaped openings placed at random as interstices between the circular cells; on the lateral surface, ribs are carinate, and describe almost perfect hexagons near their outer limits, while the cells they delimit near the bottoms of the ribs are nearly circular; the side walls of the ribs in this area have delicate vertical tracings which show a (micro-) pentagonal arrangement.

The micropyle consists of six large openings on a smooth surface (Fig. 21) which is quite outwardly convex; the rosette is barely discerned by negative outlines around the petals in an otherwise unstructured surface; the circular micropylar area is 0.08 mm in diameter and is slightly convex, bowed upward from the surrounding transition zone collar.

No aeropyles were noted leaving us to speculate whether or not the enlarged micropyles may serve in this capacity in this species.

Emesis mandana furor Butler and Druce
Fig. 4
d. 0.96 mm; h. 0.32 mm

Egg circular in horizontal section, dome shape in profile with the micropylar area (diameter 0.19 mm) slightly depressed into the apex of the dome; egg slightly wider, but not as high (in relation to its width) as other *Emesis* species; chorionic network highly reticulate, with hexagonal cells resembling a honeycomb covering all visible surfaces except the micropyle; the cells are arranged in a regular manner, appearing to be in linear or gently curving rows without, however, assuming repeatable patterns; cells largest at shoulders and upper sides, becoming smaller as they approach the micropylar region, where they are reduced to one-quarter size and become slightly distorted in shape as they "roll over" the lip of the slight vertical drop to the micropylar margin; spiny processes up to 0.04 mm long protrude from the rib intersections surrounding each cell so that the six cellular spines give a distinct echinoid appearance to the chorion; the spines are largest on the sides and shoulders, reduced on top, and are wanting near the apex; a carina runs along the crest of each rib and starts to run up the base of each spine before gradually disappearing; side cells have a convex shape, and a smooth surface, even though several folds or pleats run from the rib bases towards the center or lowest part of the cell.

Micropyle with eight holes arranged in circle; rosette difficult to detect; micropylar area of irregular or semi-undulating surface level with numerous pores of a size slightly larger than the micropyles.
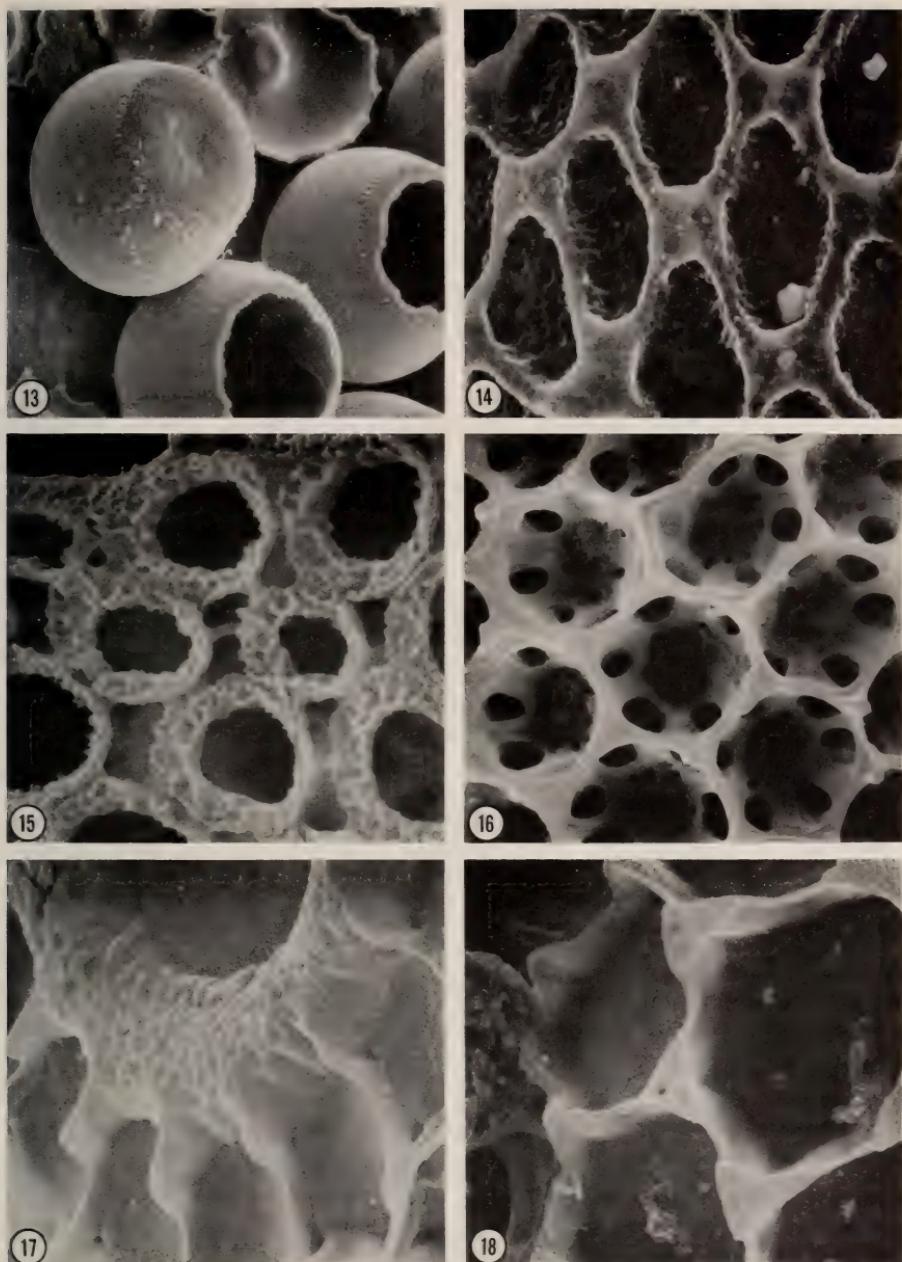
FIGS. 13–18. Eggs of Riodinidae and Lycaenidae. **13,** *Euselasia hieronymni* hatched and unhatched eggs, 60×; **14,** Porous plastron in *Brephidium pseudofea,* 600×; **15,** Rib surfaces in transition zone of *Emesis emisea,* 1800×; **16,** Inverted funnel-shaped meshwork and aeropyles in *Emesis tegula,* 360×; **17,** Flying buttress ribs near collar of *Calephelis rawsoni,* 300×; **18,** Aeropyles on rib junctures, lateral area of *C. rawsoni,* 360×. Photographs reduced to 0.58 or original size.

Emesis tegula Godman and Salvin

Figs. 5, 16, 23
d. 0.90 mm; h. 0.50 mm

Shape and external appearance much like *mandana*, only with a higher profile; cells of honeycomb reticular network shaped like inverted bowls with six large openings on lateral margins (Fig. 16) and numerous small pores on convex bottom; broad carina on ridges; thin spine or needle-like process protruding outward from each rib juncture; most of these spines are slightly recurved at their tips.

Micropyle with five holes; rosette uniquely set on an elevated hillock or pimple projecting upward from the floor of the micropylar area (Fig. 23); the elevation is so modest that this character is not visible dorsally, the specimen must be tilted slightly; petals of rosette outlined by delicate elevated ribs; micropylar surface pitted with pores which are much larger than the micropyles.

Emesis tenedia C. & R. Felder

Fig. 6
d. 0.72 mm; h. 0.40 mm

Shape and external appearance much like *mandana* and *tegula*, but generally smaller; central micropylar depression smaller (0.07 mm) and more bowl-like; transition zone between micropylar area and hexagonal cells composed of small cells whose outlining walls are relatively thick and sloping; cells on shoulder and side of the type found in *tegula*, but the central "bottom" of the pit is deeper; the large pores on the sides of the cells are often "closed," perhaps by accessory gland secretions which cover the entire egg surface during oviposition rather than just the side adhering to the plant substrate; spines projecting from the rib intersections not as long on the sides as in *mandana*, so that the dorsal view may not appear as echinoid.

Micropyle with seven or eight holes at the bottom of a gently-rounded micropylar pit; the rosette is slightly elevated above surrounding areas, though not on a hillock as in *tegula*.

Apodemia mormo mejicana (Behr)

Figs. 9, 19
d. 0.92 mm; h. 0.60 mm

Shape and profile as in *Emesis tegula*; hexagonal cells in the form of honeycomb reticulations on all visible surfaces except micropylar area; needle-like projections at rib intersections are recurved (this character may be exaggerated by artifacts induced by handling, perhaps more so in newly laid eggs); carina on ridges between spines; cells are deeply concave, cup-shaped, with open, rather large pores in lateral walls; no abrupt demarcation between rib walls and cell sides; cells adjacent to micropylar region smaller and distorted from hexagon to odd shapes tending toward the oblong; transition zone seems to be overlaid with viscous cement which on hardening, covers the ribs and cells adjacent to the micropylar region (Fig. 9) and looks artifactual.

Micropyle of five holes; rosette not distinct, seven to ten petals of a recessed type (Fig. 19); micropylar region smooth except for a suggestion of hexagon shape cells through slight depression or elevations in the surface.

Apodemia chisosensis Freeman

Figs. 10, 24
d. 0.93 mm; h. 0.48 mm

Shape and appearance much like *A. mormo*; markedly echinoid in gross view as the spiny processes at each rib intersection approach 0.04 mm length on lateral margins; ribs carinate, depressed slightly as they run between spines such that a line drawn from the tip of one spiny process to another along the surface would form a "U" shape, with the rib forming the bottom of the "U"; cells deeply inverted; large lateral pores
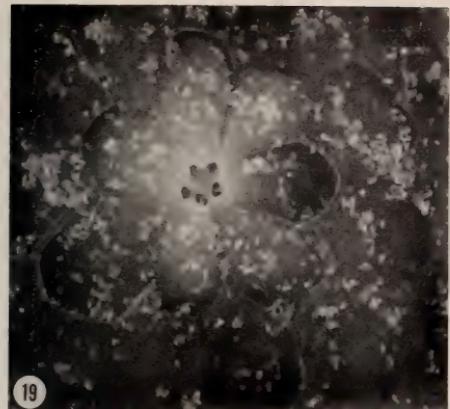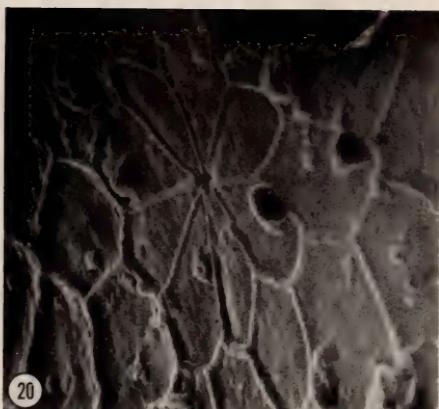
FIGS. 19–24. Micropylar regions in eggs of Riodinidae. **19,** *Apodemia mormo mejicana*; detritus on surface results from alcohol preservation, 1200×; **20,** *Lasaia sula penninsularis,* note delicate ribbing of rosette, 960×; **21,** *Emesis emisea,* depressions or troughs form rosette, 1200×; **22,** 3-hole micropyle of *Apodemia palmeri,* 1200×; **23,** *Emesis tegula* with rosette area elevated, 600×; **24,** Collar-like, lacey network surrounding micropyle in *Apodemia chisosensis,* 360×. Photographs reduced to 0.58 of original size.

almost as deep within cells as spines are high; many smaller pores in the bottom of the inverted bowl-shaped cell may serve as aeropyles.

Micropyle of 4–5 pores; four petal rosette very difficult to detect and almost obsolete; entire micropylar area and adjacent transition zone overlaid with smooth-surfaced coating which is highly porous near its margins (Fig. 24) giving it a "lacey" appearance; the elevation of the margins of this coating suggest that it was laid down after the ribs and cells were formed perhaps in an overgenerous matrix which originally delivered sperm to the micropyle.

This micropylar coating in *Apodemia mormo* and *chisosensis*, in addition to other egg characters shared by them, distinguishes them from eggs of their congeners described below.

Apodemia palmeri (Edwards)
Figs. 11, 22
d. 0.68 mm; h. 0.34 mm

Egg circular in top view, dome-shaped in profile without marked flat surface on top; micropylar area sharply depressed with transition zone having a perpendicular surface adjacent to micropylar region; ridges are broad, with thin carina at crest (becoming obsolete in spots, more apparent at rib intersections) and gradually sloping walls; cells gently depressed with six large pores on lateral margins beneath rib intersections; bottom of cells of irregular surface with many scattered small pores.

Micropyle with 3 or 4 holes; rosette present but nearly obsolete (Fig. 22).

Apodemia walkeri Godman and Salvin
Fig. 12
d. 0.72 mm; h. 0.38 mm

Shape, size and profile, as in *A. palmeri*; micropylar depression in apex of top 0.20 mm (twice as large as *palmeri*); ridges between cells rounded, with carinae, mostly limited to lateral areas where they help form stubby nipples at rib intersections; cells rather deeply concave with lateral fluting formed by up-side down tear-drop indentations separated by ribs confluent with lateral margins of ridges above (the cells resemble the die fitted by a Phillips head screwdriver); cells in transitional zone one-quarter to one-half size of more lateral cells, and of irregular to almost closed shape.

Micropyle with 4 or 5 holes; rosette not apparent in several eggs observed.

Euselasia hieronymni Godman and Salvin
Fig. 13
d. 0.50 mm; h. 0.40 mm

Egg circular from above, shaped like an upright flat topped pottery jar in profile; eggs are widest at about one-third their micropylar height from the bottom (0.12–0.13 mm) and gradually curve inward to the top shoulder. The flat top surface measures 0.36 mm, or slightly less than the height of the egg; the chorionic surface is smooth, though it may be interrupted here and there with delicate chorionic tracings resembling the silken threads left by larvae; a series of aeropyles line the lateral margins of the shoulder with a tendency for the openings to occur in pairs (Fig. 13); the aeropyles are borne on small pimple-like craters. Micropyle with three openings with a depressed area between; rosette of ten broadly joined petals of the depressed type.

Fig. 13 shows hatched as well as unhatched eggs. The larvae also consume the lateral margins of the shell, and examples of these partially eaten eggs are also on the figure. On the eaten eggs can be observed the concave inner part of the ventral surface, which conforms to that reported in *Anatole rossi* Clench, by Ross, 1965. A ventral concave surface was a predicted configuration for an "unknown" lycaenid (in Downey & Allyn, 1980).

The egg of *Hieronymni* is fairly close to being as high as wide. Only one riodinid,

the European *Nemeobius lucina* L., presently is known to us, in which the height is greater than the width (0.8 mm to 0.72 mm, according to Doring, 1955, p. 98).

DISCUSSION

Having closely studied the chorionic architecture of these 13 species of Riodinidae, we are struck by the variability of different egg types compared to those in the larger family Lycaenidae. Indeed, there is probably as much diversity in egg pattern in these few species as in the 42 lycaenid genera treated by Clark and Dickson (1971), which included several subfamilies and tribes. A more exhaustive survey (if and when more of the relatively uncommon eggs become available) would be particularly rewarding from a taxonomic viewpoint. Too few species were examined here to warrant more than conjecture regarding inter-familial questions involving the Lycaenidae and the Riodinidae. However, we expected fewer differences than those noted, and our opinions have been influenced more in the direction of family separation than they were before.

Chorionic structures of the egg reflect the shape of the follicular epithelium in the ovarioles which secreted them and are thus the manifestation of an adult character. Whatever their significance for taxonomy, they should be correlated with that of other adult character states. What are unusual here are the marked differences among the few species examined. Had the latter been selected (they were not) on the basis of representing discrete and disparate taxonomic positions, we might not have been as impressed. We are now anxious to see samples of other riodinid eggs.

While smooth, relatively unsculptured eggs are commonly encountered in the Hesperiidae and Papilionidae, eggs with a highly sculptured chorion are the rule in the Lycaenidae and Riodinidae. The closest approach to the smooth condition so far observed, however, is in *Euselasia hironymni* where the only adornment on the relatively smooth egg consists of an inconspicuous, single ring of aeropyles around the circumference of the top lateral margin, plus a few irregular, web-like tracings almost in the nature of detritus on the surface. Even the European *Nemeobius lucina*, which tends toward the unsculptured condition, has a few scratches on the surface. *Euselasia* also has unusual oviposition behavior: eggs are laid in ordered clusters, rather than singly, as are the great majority of riodinid species so far known. This behavior could be correlated in an evolutionary sense with the lack of egg sculpturing. Most of the species have highly ornamented eggs with ridges, tubercles, crests and spiny elevations, easily observed with a low power hand lens.

The eggs of some congeners show sufficient diversity to suggest

further taxonomic study. The egg of *Emesia emisea* for example, is clearly distinct from those of *E. mandana, tegula* and *tenedia. Apodemia mormo* and *A. chisosensis* also are clearly related, but distinct, when compared to eggs of *A. palmeri* and *A. walkeri.*

We are struck by the lack of plastrons in the Riodinidae, since such structures are common in the Lycaenidae (Fig. 14). Most lycaenid eggs (particularly in the Theclinae, Lycaeninae, Polyommatinae and Miletinae) have much of the subsurface chorion (beneath the reticular network of ridges and tubercles) perforated by many small pores which enable the highly porous chorion to serve as an air store and plastronic network. This thin-film air mass serves as a physical gill when submerged in rain water, which is rich in dissolved oxygen. The small pores of the plastron type were only noted in *Apodemia chisosensis*, though the micropylar regions of *Emesis* species (other than *emesia*) contain pores. In the latter species we suspect micropylar respiration, particularly because of the lack of aeropyles, and pores of any other sort. Aeropyles were found in *Apodemia, Lasaia, Caria* and *Calephelis*, but the size and number of these openings was no greater than the same structures in lycaenid egg types, even though the lycaenids also are equipped with the plastronic pores.

While lacking plastrons (in general), some riodinid eggs are highly suggestive of lycaenid types. For example, *Apodemia mormo* and *A. chisosensis* resemble the eggs of temperate lycaenids, but others in the same genus (*walkeri, palmeri*) are much further removed in facies from a lycaenid type. Interestingly, there is some evidence of Nearctic speciation in both *Apodemia* and *Calephelis*, and perhaps the resemblance of egg types in some members of the former genus to lycaenid types has been attained through ecotypic convergence. *Calephelis,* however, is morphologically far removed from the lycaenid condition, whose closest approach to the hexagonal eggs would be found only in the Oriental Poritinae.

We are making some attempt to relate egg structure with adaptive strategies, but beyond such generalities as might be indicated by plastronic respiration, we have not as yet found any major differences in egg-laying strategies which correlate with these different egg structures.

LITERATURE CITED

CLARK, G. C. & C. G. C. DICKSON. 1971. Life histories of the South African lycaenid butterflies. Purnell, Cape Town. XVI + 272 p.

DORING, E. 1955. Zur Morphologie der Schmetterlingseier. Akademie Verlag, Berlin. 154 p. + 61 tables.

DOWNEY, J. C. & A. C. ALLYN. 1980. Chorionic sculpturing in eggs of Lycaenidae. Part 1. Bull. Allyn Mus., in press.

ROSS, G. N. 1965. Life history studies on Mexican butterflies. II. Early stages of *Anatole rossi* a new myrmecophilous metalmark. J. Res. Lepid. [1964] 3(2): 81–94.

DESCRIPTION, NATURAL HISTORY, AND DISTRIBUTION OF A NEW SPECIES OF *ERETRIS* (SATYRIDAE) FROM COSTA RICA

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ABSTRACT. *Eretris suzannae* (Satyridae) is described as a new species from Costa Rica. It is compared with the other three species of Central American *Eretris*. The natural history and distribution of *E. suzannae* are described, with reference to the restricted habitat where it occurs.

The Neotropical genus *Eretris* (Satyridae: Pronophilinae) is a montane group which has its highest species diversity in the South American Andes but which ranges as far north as Guatemala. Three Central American species are recorded in the literature, of which one is of dubious occurrence. During my studies on the butterfly fauna of Costa Rica I acquired a thorough knowledge of Costa Rican butterflies. When comparing my material with material in the major world museums and in the literature, I found an undescribed species of *Eretris*. In this paper I describe *Eretris suzannae* as a new species and present my observations on its natural history in Costa Rica.

Eretris suzannae DeVries, **new species**

Description. **Eyes** densely hairy. **Antennae** rufous, very sparsely scaled, basal quarter dorsally scaled dark brown, terminal three segments of the club fuscous with a few white scales at the extreme tip, each segment ringed with a fuscous band anteriorly.

Male. Upperside ground color fuscous, darker in the broad discal androconial area; submarginal dark faint line, extending on each wing from apex to tornus. **FW underside:** ground color fuscous; a dark slightly wavy postbasal line located about $\frac{1}{5}$ of way from wing base, running from Sc to 2A; within cell the line is slightly convex, crossing cell to Cu_2, then more irregular and fainter to 2A; postmedial line dark, wavy, running from near costa to 2A about $\frac{3}{4}$ of way from base; ground color of area beyond postmedian line lighter, with faint subapical greyish scaling; an irregular submarginal line runs from costa to 2A, a thin marginal band runs from R_2 to 2A, slightly rufous; basal edge of this band with a fine dark line. **Fringe** black interspaced with grey. **HW underside:** ground color fuscous; a dark postbasal line runs straight from costa about $\frac{1}{3}$ of way from base, through cell, angled basally below posterior cell margin, crossing cell Cu_2-2A and terminating within anal cell about $\frac{1}{3}$ of way from base; an irregular postmedial line runs from costa at $\frac{2}{3}$ of way to just basad of tornus; a little over half way from this line to margin a wavy submarginal line, black anterior to subtornal ocellus, rufous posterior to it; area between postmedian and subterminal lines lightly greyish; a subapical ocellus between Rs and M_1, interrupting the postmedian line, black with small white central pupil, ringed thinly with tawny; a much larger subtornal ocellus between Cu_1 and Cu_2, interrupting the submarginal line, with a minute white pupil distad of center and a thin, tawny ring that distally just touches the marginal band; a minute rufous pupillate ocellus between postmedian and submarginal lines,

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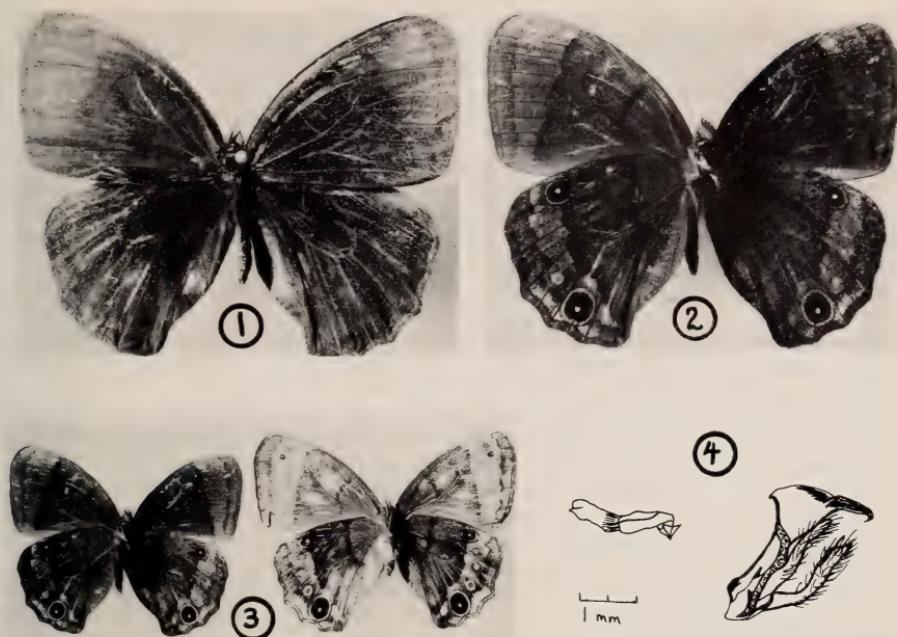
FIGS. 1–4. *Eretris suzannae*. **1,** dorsal aspect of paratype ♂; **2,** ventral aspect of paratype ♂; **3,** ventral aspects of both sexes, male (left) and female (right), both are paratypes. Note the higher contrast of color in the female; **4,** drawing of entire male genitalia.

nearer the latter, in cell M_3-Cu_1; a thin rufescent marginal band runs from apex to tornus; inner margin and tornal area basad to postbasal line with a rufous blush; ground color greyish from M_3 to 2A between submarginal line and marginal band. Fringe same as on FW.

Female differs from the male as follows: **HW upperside:** pupillate ocellus present near tornus corresponding to the one on the underside but smaller, ringed with a thin band of rufous. Tornal and submarginal area dull rufous. **FW underside:** a row of two or three additional submarginal ocelli, at times faint, in Cu_1-M_3, M_3-M_2, and M_2-M_1. A minute white dot between M_1 and R_5. Postbasal, postmedial, and submarginal lines more rufous. **HW underside:** ground color much more rufous, the whole appearance much richer and more contrasting; subapical and tornal ocelli larger with a row of four tiny ocelli between them; distal greyish scaling much more pronounced.

Variation. Variation among males is common, involving presence or absence of tiny subapical ocelli on the FW underside between postmedial and submarginal lines, frequent presence of one or more minute submarginal ocelli between the larger subapical and tornal ocelli on the HW underside, and the occasional presence of a faint tornal ocellus on the HW upperside.

Length of forewing. ♂, 23.0 to 25.2 mm (n = 20); ♀, 26.0 to 26.3 mm (n = 8).

Types. Holotype: ♂, Costa Rica, San Jose Prov. 900 m, Parque Braullio Carrillo, 30 June 1978; leg. P. J. DeVries. (Figs. 1–4). Paratypes: All from Costa Rica, leg. P. J. DeVries except as noted otherwise. In (MNCR): 4 ♂, same data as the Holotype; the following from the same locality as Holotype: ♂, 10 April 1977, ♂, 6 August 1977, ♂, 20 August 1977, ♀, 17 December 1977, ♀, 6 November 1976, leg. F. G. Stiles; ♂, vicinity of La Cinchona on Sarapiqui road, 1200 m, Heredia Prov., 20 June 1976; 2 ♂, Peñas Blancas valley near Monte Verde reserve, 1300 m, 19 February 1978. In

(CM): ♂, Tres Rios, Cartago Prov., Aug. (no date), leg. W. Schaus. In (USNM): 2 ♂, Carillo, May, leg. W. Schaus; ♂, San Geronimo, Oct., leg. W. Schaus, ♀, Carillo, Oct., leg. W. Schaus; ♀, Mount Poas, April, leg. W. Schaus. In (BMNH): 2 ♂, Bajo la Hondura, San Jose Prov., 30 June 1978, leg. P. J. DeVries, ♀, San Geronimo, leg. W. Schaus; ♀, Carillo, leg. Underwood. In (GBS): ♂, Rio Sarapiqui, 1300 m, 26 June 1976, leg. G. B. Small; ♀, Rio Sarapiqui, 1300 m, 27 June 1976, leg. G. B. Small.

Disposition: The Holotype has been placed in the Allyn Museum of Entomology; paratypes in the Museo Nacional de Costa Rica (MNCR), Carnegie Museum (CM), U.S. National Museum (USNM), the British Museum (Nat. Hist.) (BMNH), and the private collection of Gordon B. Small in Panama (GBS).

Etymology. I name this species in memory of my late sister Suzannae Mary DeVries.

Comparison with Central American *Eretris.* The three other Central American species of *Eretris* (*E. hulda* Butler and Druce, *E. subrufescens* Grose-Smith and Kirby, and *E. maria* Schaus) differ from *E. suzannae* in the following ways:

E. hulda, known from Costa Rica and Panama, never has large ocelli on the HW underside and has a wavy postmedial HW band that expands from the tornus as it progresses toward the cell. Appressed to the basal margin of this postmedial band is an irregular, thin medial line of golden brown. Although variable to a slight degree, the above characters are constant and unmistakable. (See Seitz Pl. 56c and Godman and Salvin Pl. 9, nos. 7 and 8 for illustrations.) *E. hulda* in Costa Rica inhabits high montane forest habitats and is in greatest abundance between 2400–3000 m elevation. In five years' fieldwork I have not found *E. suzannae* and *E. hulda* flying together. Of the Central American species, *E. hulda* is the most abundant in collections and is certainly the most common in Costa Rica and Panama.

E. subrufescens was described from a single specimen labeled "Costa Rica." The type is in the BMNH. Besides the type specimen I have seen no specimens from Central America in collections or in the field; the bulk of the material is from Colombia. These facts lead me to believe that *E. subrufescens* is of dubious occurrence in Central America. Specimens seen by me have a submarginal row of tiny black dots (ocelli) on the HW underside set in a blush of wide rufous along the distal ⅓. This species lacks pupillate ocelli. See Seitz pl. 56c and Grose-Smith and Kirby, 1892–1897 (original description) for illustrations. In the USNM and CM *E. suzannae* was incorrectly determined (det. Schaus) as *E. subrufescens.*

E. maria was described by Schaus (1920) from Volcan Santa Maria in Guatemala. Very few specimens are known, and all are from the Guatemalan type locality. This species is phenotypically most similar to *E. suzannae,* but differs consistently by two tiny tornal ocelli on the underside of the HW (both sides in the female) being less darkly fuscous, being smaller in size, with the ocelli round and not ovoid, and having the pupils centralized not eccentric. The genitalia of the two species differ in that *E. maria* has the gnathos longer and straighter, the penis longer and more strongly bowed, the harpe with a gentle upward curve and not with an angle; the dorsal portion of the tegumen is flatter and not so dome-shaped as in *E. suzannae,* giving the interface between the tegumen and the uncus a flatter angle.

Natural History. In Costa Rica, *E. suzannae* occurs locally along ravines and mountain pass habitats between 900–1300 m elevation. My field observations of *E. suzannae* over four years indicate that it is restricted to a narrow transitional habitat on the Atlantic drainage between montane cloud forest and the foothills of the Cordillera Central. This habitat, which I term the "Carrillo belt," shows a high degree of endemism and biotic peculiarity for butterflies (pers. obs), birds (F. G. Stiles, pers. comm.), Orthoptera (H. Rowell, pers. comm.), and ferns (L. D. Gomez, pers. comm.) in contrast to other areas of Costa Rica. This perhaps is an indication that *E. suzannae* is an endemic Costa Rican species although it may be found in northern Panama. The known distribution of *E. suzannae* is shown in Fig. 4. The "Carrillo belt" is fairly well outlined by the cluster of localities around the locality Bajo la Hondura which constitutes a belt of volcanoes.
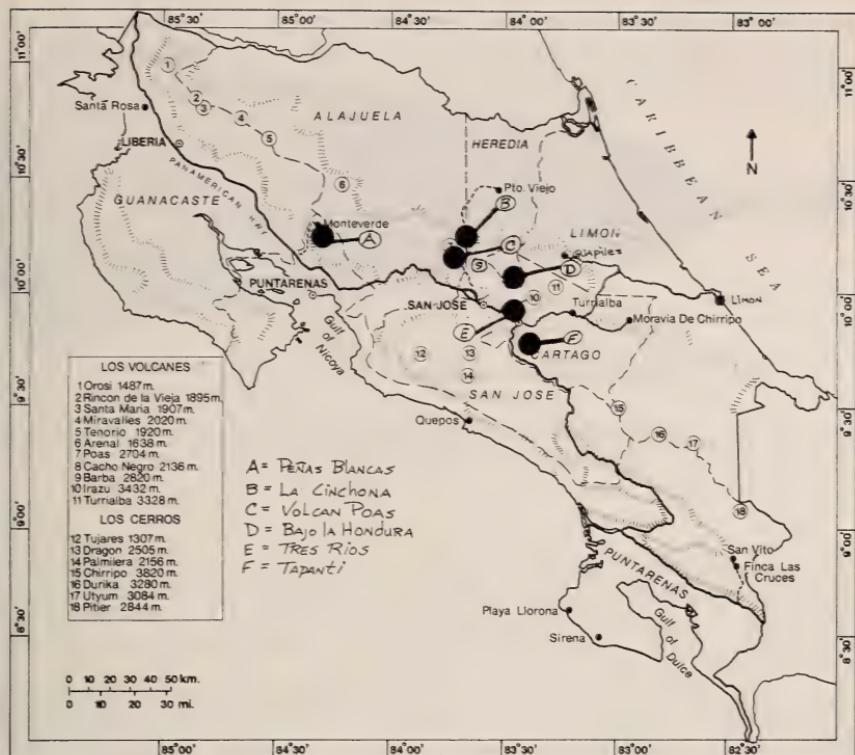
FIG. 5. Known distribution of *Eretris suzannae* in Costa Rica. Explanations of the capital letter locality plotting are as follows: **A**—Peñas Blancas. This locality is the farthest north that *E. suzannae* has been traced. The habitat where the collections were made is below the mountain pass in the Monte Verde Forest Reserve on the Atlantic drainage and represents a continuation of the "belt" that runs along the Cordillera Central where *E. suzannae* is confined. **B**—La Cinchona. Along the Sarapiqui road at the edge of the steep ravine where the Rio de la Paz I have seen, is located on the Atlantic slope of Volcan Poas below the cloud forest within the "belt" mentioned in the text. **C**—Volcan Poas. The author has not seen *E. suzannae* on the Volcan. I include this locality due to the specimens labeled as such in the collection of W. Schaus in the USNM. **D**—Bajo la Hondura. The type locality located in the mountain pass between Volcan Barba and Volcan Irazu. This habitat typifies the belt of endemism. In collections of Lepidoptera made at the turn of the century there are many specimens from Costa Rica labeled "Carillo" which, judging from the species I have seen, included the Bajo la Hondura locality. In actuality Carrillo is below 300 m and has no resident high elevation species. **E**—Tres Rios. Located on the Pacific slope of Volcan Irazu and at one time was an extension of the forest typical of the "belt." **F**—Tapanti. In the Talamanca mountain range at the interface of the Talamancas and the Reventazon Valley where there is a sun shadow habitat atypical of the surrounding forest. In this habitat other endemic Costa Rican butterflies are known although it is not part of the Carillo belt of endemism.
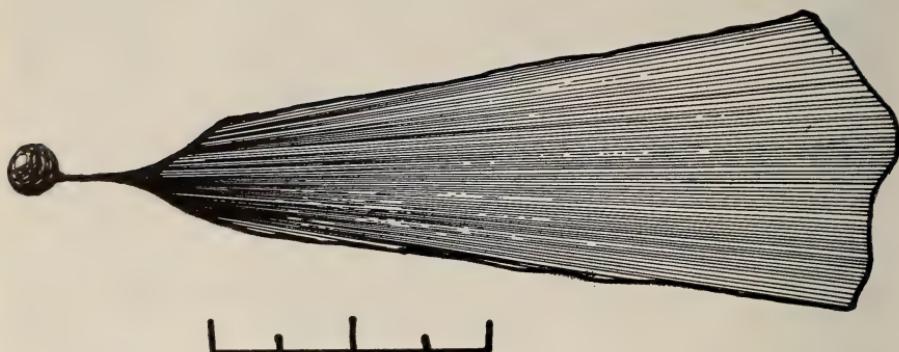
FIG. 6.   Illustration of the oviposition site of *E. suzannae* on the terminal spine of the hostplant leaf. Drawn from a photograph. Full scale line = 1 cm.

In association with *E. suzannae* are the following satyrid butterflies: *Cyllopsis rogersi* Godman and Salvin, *C. vetones* Godman and Salvin, *Pedaliodes cremera* Godman and Salvin, *P. perpena* Hewitson, *Catargynnis rogersi* Godman and Salvin, *Oxeoschistus puerta submaculatus* Butler and Druce, *Drucina leonata* Butler, and *Oressinoma typhla* Westwood and Hewitson.

E. suzannae flies all year in the vicinity of its hostplant, *Chusquea* sp. (Bambusaceae), a tall bamboo (up to 15 m) that grows along the edges of ravines. The butterfly darts in and out of the *Chusquea* thickets or sails over the tops of them along flyways, interacting with other satyrid butterflies by chasing and circling. The butterfly stays very close to the thickets. Flight periods are restricted to hours of sunshine which normally occur from about 0730 to 1230 h. After this time, cloud cover builds up and obscures the sun.

Adult butterflies feed on fungi that grow on fallen tree trunks and rotting wood, probably Mucorales and Thelephorales. They also feed on the fallen and unfallen fruits of *Clusia* sp. (Guttiferae), the flowers and fruits of *Satyria warzewiscia* (Ericaceae), and an unidentified melostomaceous tree.

Oviposition takes place any time of day during sunshine. A single egg is laid on the terminal spine of a *Chusquea* leaf (Fig. 6) as is done by a number of the high elevation tropical satyrids (pers. obs.). The egg is pale green and very cryptic on the hostplant. After oviposition the female flies a short distance (2–10 m) from the oviposition site and rests with her wings open for 2–5 minutes in a sunny spot. She then flies to the hostplant and immediately oviposits again. This entire process is repeated. I watched one female repeat this behavior eight separate times after which she moved down the ravine and out of sight. The eggs hatch after four to five days. The first instar larvae eat the egg shells. The following day they begin eating the *Chusquea* leaf. The first instar larvae are pale green with black, unforked head capsules, measuring approximately 4 mm. More details about the early stages will be presented in a later report.

comparing material in the BMNH, and to the following persons for assistance in the field: C. Todzia, F. G. Stiles, M. Singer, P. Ehrlich, R. Sanford, G. B. Small, W. Hallwachs, L. D. Gomez, and B. A. Blake.

LITERATURE CITED

GODMAN, F. D. & O. SALVIN. 1879–1901. Biologia Centrali Americana. Lepidoptera: Rhopalocera, vol. 1, 1879–1886 (Satyridae, 1881), I–XLV & pp. 1–487; Vol. 2, 1887–1901, pp. 1–782; Vol. 3, 1879–1901, plates 1–112.

GROSE-SMITH, H. & W. F. KIRBY. 1892–1897. Rhopalocera Exoctica vol. 2. Gurney & Jackson, Paternoster Row, London. (coll. of articles with individual pagination).

SCHAUS, W. 1920. New species of Lepidoptera in the United States National Museum. Proc. U.S. Nat. Mus. 57: 107–152.

WEYMER, G. 1910–1912. In A. Seitz, ed. Macrolepidoptera of the World. vol. 5. Alfred Kernan, Stuttgart. pp. 173–283.

A REVIEW OF THE GENUS *HYPOTHYRIS* HÜBNER (NYMPHALIDAE), WITH DESCRIPTIONS OF THREE NEW SUBSPECIES AND EARLY STAGES OF *H. DAPHNIS*[1]

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ABSTRACT. The Neotropical genus *Hypothyris* (Lepidoptera: Nymphalidae: Ithomiinae: Napeogenini) is regarded on biosystematic grounds, as including 16 species divided into 137 geographical subspecies (34 still undescribed). The distributions of *Hypothyris* subspecies have been used to help define centers of butterfly endemism (at the lowest recognized taxonomic level) in the Neotropical forests; these correlate well with areas of high probability for forest continuity during the cool-dry spell at the end of the Würm-Wisconsin glaciation, 13,000–20,000 years ago. Three new subspecies described for the little-known *H. daphnis* D'Almeida extend its range to Amapá, extreme northwestern Pará, southern Maranhão, and the lower Rio Madeira. The early stages of the new subspecies from Amapá (illustrated) are similar to those of other solitary-feeding species of *Hypothyris*.

Fox & Real (1971) revised the Neotropical genus *Hypothyris* Hübner (Napeogenini). This revision was concluded under extenuating circumstances, after the death of the senior author and with limited access to important type material in British and continental museums; nevertheless, it was a major step in understanding the systematics of these mimetic butterflies.

Recent fieldwork in the Neotropics and visits to the British Museum (Natural History) led to a new revision of the biosystematics of the genus and the relation of natural biogeographical units to taxonomic names. This work was presented as a preliminary reorganization of Fox and Real's order for the genus (Brown, 1977). This supplementary revision has now been further refined (Brown, 1979; Mielke and Brown, 1979) by additional field and museum study, especially the examination of Haensch and Weymer types in the Museum für Naturkunde (Humboldt-Universität, Berlin). The new biosystematic vision of this complex genus, including 16 species and 137 subspecies (34 of them undescribed), is supported by morphological studies and the discovery of intergrading populations in narrow hybridization zones between subspecies (Figs. 1–12; Appendix). Final definition of this genus and of other genera in the tribe will only be possible,

FIGURE 1: Reorganization of _Hypothyris_

Fox & Real (1971)   Brown (1979)

NINONIA connexa, mutilla, ninonia,
  leprieurii, completa, neimyi,
  caquetacola, apollinis, antonina,
  aetha, cornelie

FIMBRIA fimbria, granadensis,
  ninyas

VALLINA vallina, colophonia

PELLUCIDA pellucida, colosseros

DIPHES

DAETA

DAETINA

METERUS zephyrus, meterus, deemae

FULMINANS fulminans, satura,
  angelina, tessmanni, satterwhitei
  virgilini

DAPHNIS daphnoides, daphnis

AEMELIA (sic)

SEMIFULVA

SOROR

ANTONIA

FLUONIA berna, pardalina,
  fulvifascia, fluonia, flavigera,
  viola, iberina

HYGIA hygia, violantilla

ROWENA

VALLONIA

GEMELLA

EUCLEA leucania, caldasensis,
  intermedia, micheneri, peruviana,
  callanga, nina, forbesi,
  euclea, barii

PYRIPPE

LATEFASCIATA latefasciata, poemne

MAMERCUS polymnides, mamercus,
  maenas

AMICA putumayoensis, amica, klotsi,
  pallisteri, meteroides, dalmeidai

MANSUETUS moebiusi, mansuetus

PHILETAERA philetaera, neustetteri,
  nemea, surinamensis, ignorata,
  michaelisi

LAPHRIA

ANASTASIA anastasia, anastasina,
  zeros, medea, niphas

HONESTA aureata, honesta,
  bicolora, arpi, acreana

LYCASTE dionaea, callispila,
  lycaste, fraterna, limpida,
  mergelena, limosa

THEA theatina, thea, vestita,
  mayi

CATILLA

GLABRA glabra, carvalhoi

    "Problematics"

Napeogenes seminigra

Hypothyris manaos

* = studied in the field

NINONIA granadensis, fimbria, diphes,
  latipennis,*ssp.nov., aetha,
  *cornelie,*mysotis,*colophonia,
  *ssp.nov.,*completomaculata,
  *mutilla,*completa,*latifasciata,
  *ninonia,*ssp.nov.,*neimyi,
  *ssp.nov., ssp.nov.,*apollinis,
  *evanescens,*daeta

METERUS zephyrus, meterus, deemae,
  ssp.nov.

CONNEXA lema, connexa,*ssp.nov.

GEMELLA gemella,*ssp.nov.,*ssp.nov.

DAPHNIS *amapaensis,*clenchi,
  *daphnoides,*daphnis,*madeira

FLUONIA *ssp.nov.,*rowena,*berna,
  uchiza,*pardalina, seminigra,
  *viola, hygia,*ssp.nov.,*manaos,
  *ssp.nov.,*iberina,*flavigera,
  fluonia, fulvifascia,*violantilla

VALLONIA *ssp.nov.,*glycon,
  *vallonia,*ssp.nov.

SEMIFULVA fulminans, putumayoensis,
  *satura,*semifulva,*pallisteri,
  *angelina, meteroides, virgilini,
  *dalmeidai,*soror

MOEBIUSI *moebiusi, ssp.nov.,
  unicolora

MANSUETUS *amica, klotsi, mansuetus

MAMERCUS polymnides, *mamercus,
  *pyrippe, ssp.nov., maenas,*ssp.
  nov., poemne,*ssp.nov.,*ssp.nov.

THEA ssp.nov.,*ssp.nov.,*thea,
  *mayi,*theatina

LEPRIEURI ssp.nov.,*ssp.nov.,
  *catilla,*ssp.nov., ssp.nov.,
  nemea,*michaelisi, leprieuri,
  *ssp.nov.,*ignorata,*ssp.nov.,
  *ninyas,*ssp.nov.

EUCLEA *valora, ssp.nov.,*leucania,
  *philetaera,*caldasensis,*euclea,
  *intermedia,*napona,*ssp.nov.,
  *hemimelas,*pachiteae,*peruviana,
  *callanga,*nina,*forbesi,*barii,
  *interrupta,*ssp.nov.,*laphria

LYCASTE dionaea, callispila,*lycaste,
  *mergelena,*limosa,*antonia,
  *limpida,*fraterna, glabra

ANASTASIA *honesta, bicolora,
  *anastasina, acreana, arpi,
  *niphas, castanea, anastasia,
  *porsenna

RHODUSSA CANTOBRICA carvalhoi

however, after extensive additional biological work and experimentation.

The genus _Hypothyris_ was among the most useful in the isoline determination of endemic centers for butterfly subspecies in the Neotropical forests (Brown, 1979, 1980; see Fig. 13). Of the 62 discrete

FIGURE 2
Subsp. of *Hypothyris ninonia*

FIGURE 3
Hypothyris meterus, connexa, thea
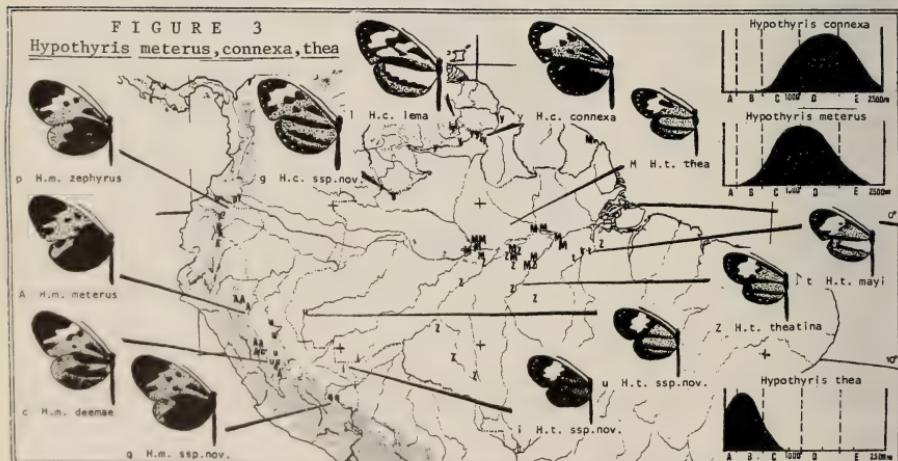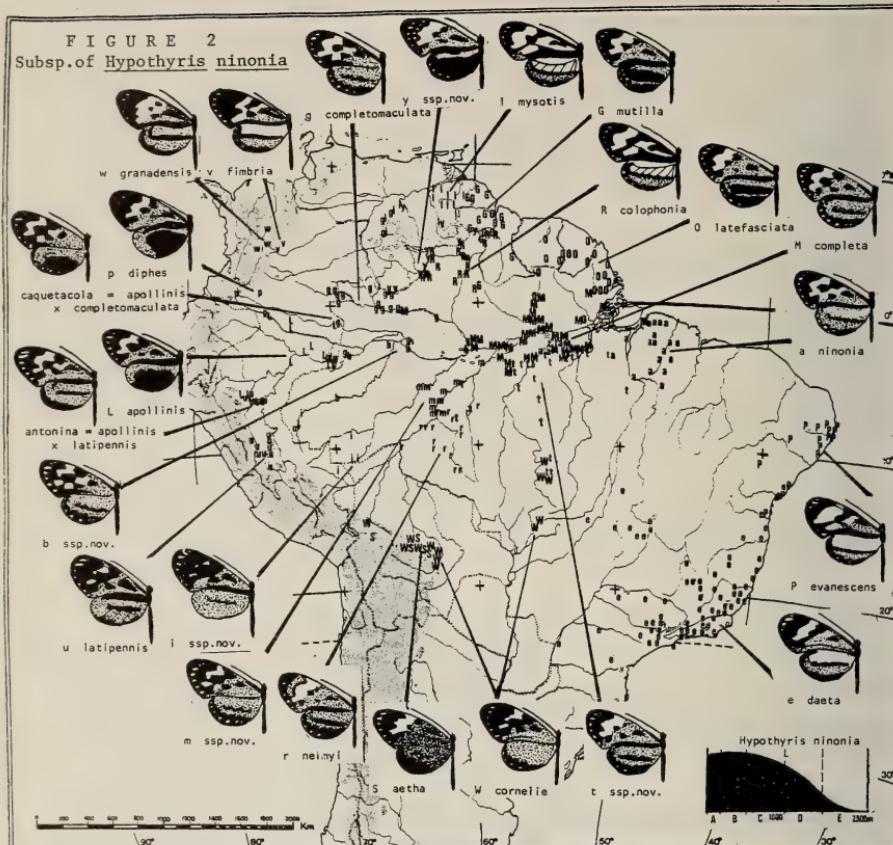
FIGURE 4
Subspecies of Hypothyris fluonia
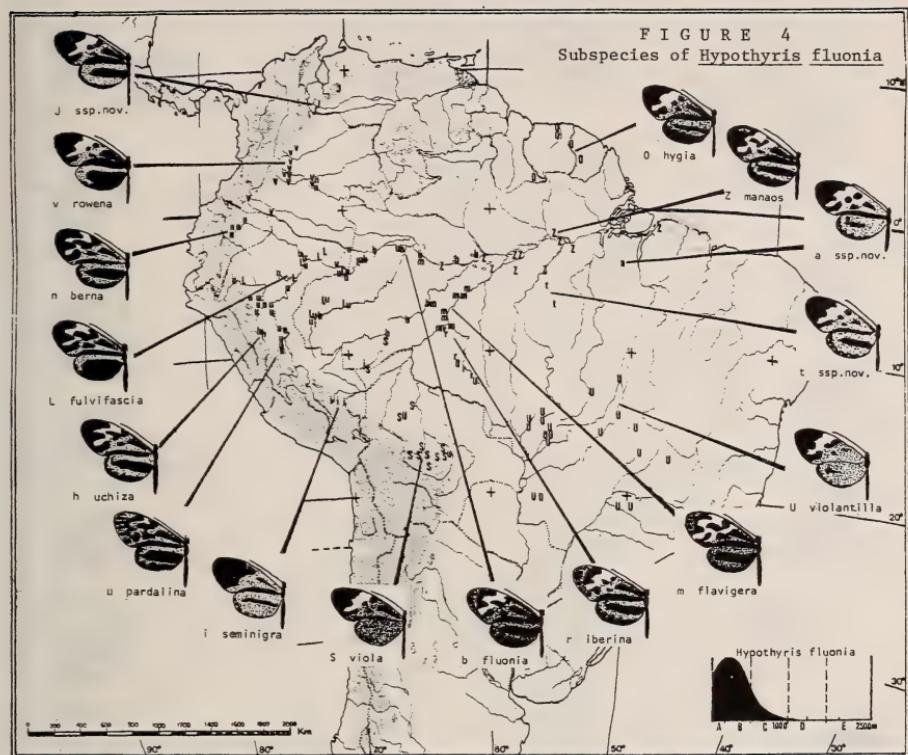
FIGURE 5
Hypothyris vallonia & semifulva

FIGURE 6
Hypothyris gemella, daphnis & mansuetus

FIGURE 7
Subspecies of Hypothyris moebiusi

FIGURE 8
Hypothyris leprieuri

FIGURE 9
Hypothyris mamercus
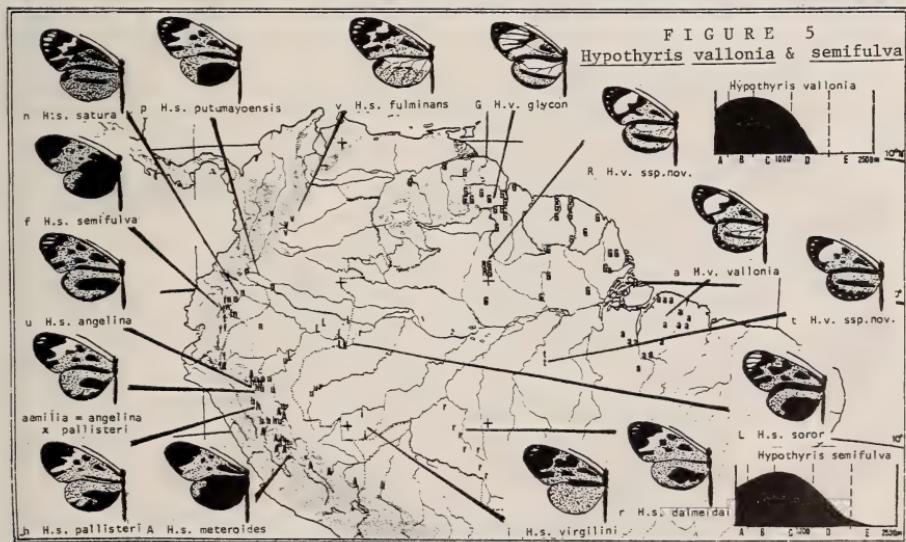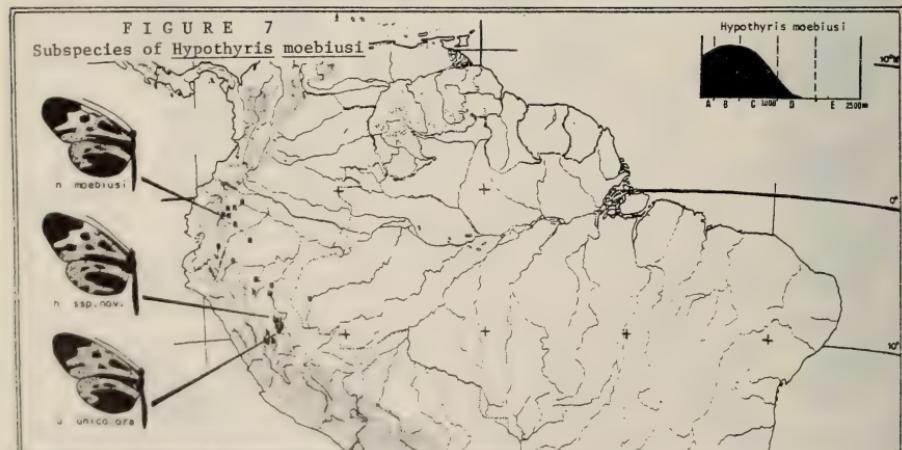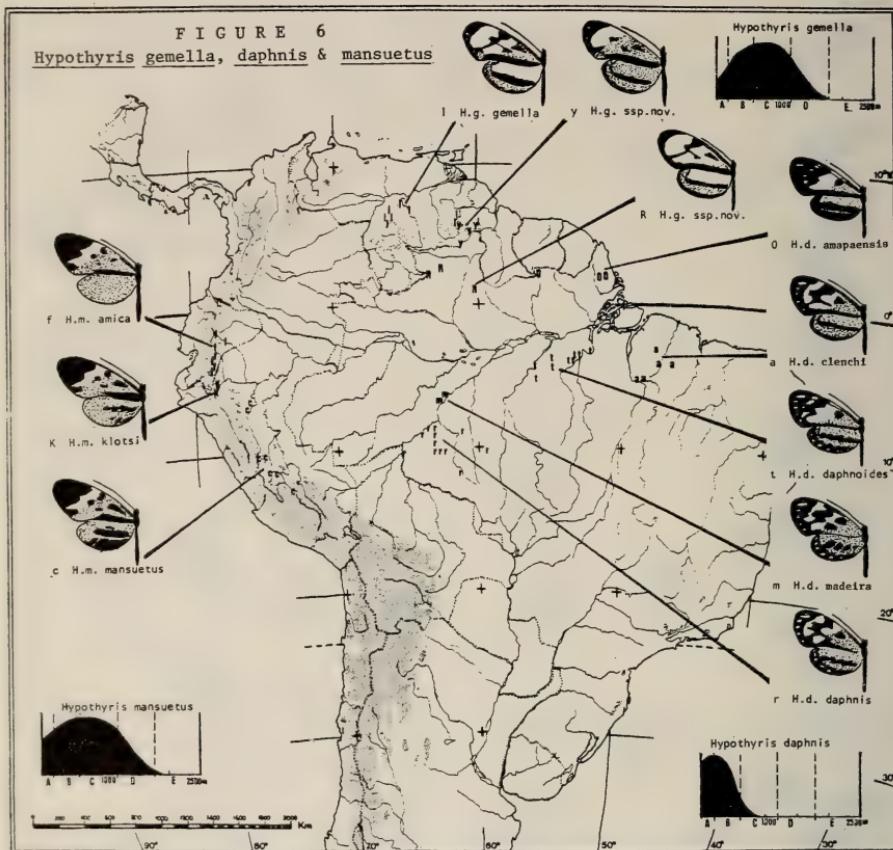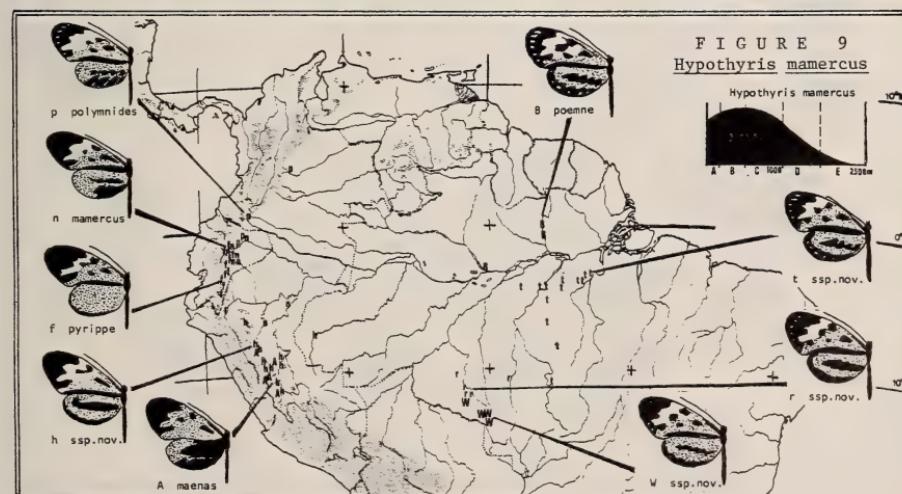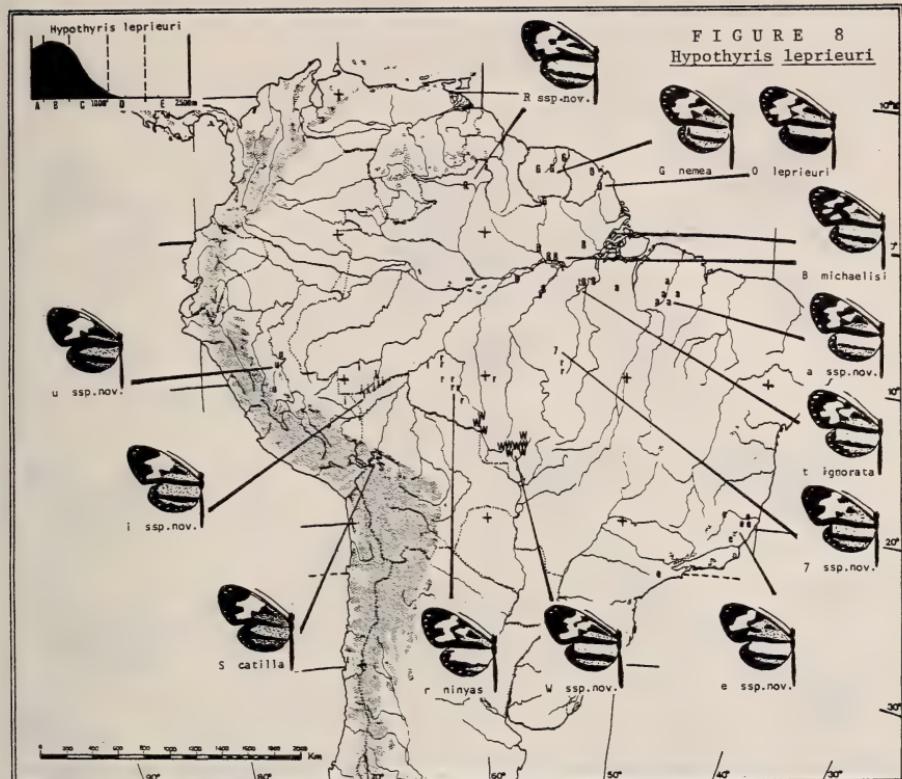
FIGURE 10
Distribution of the subspecies of Hypothyris euclea
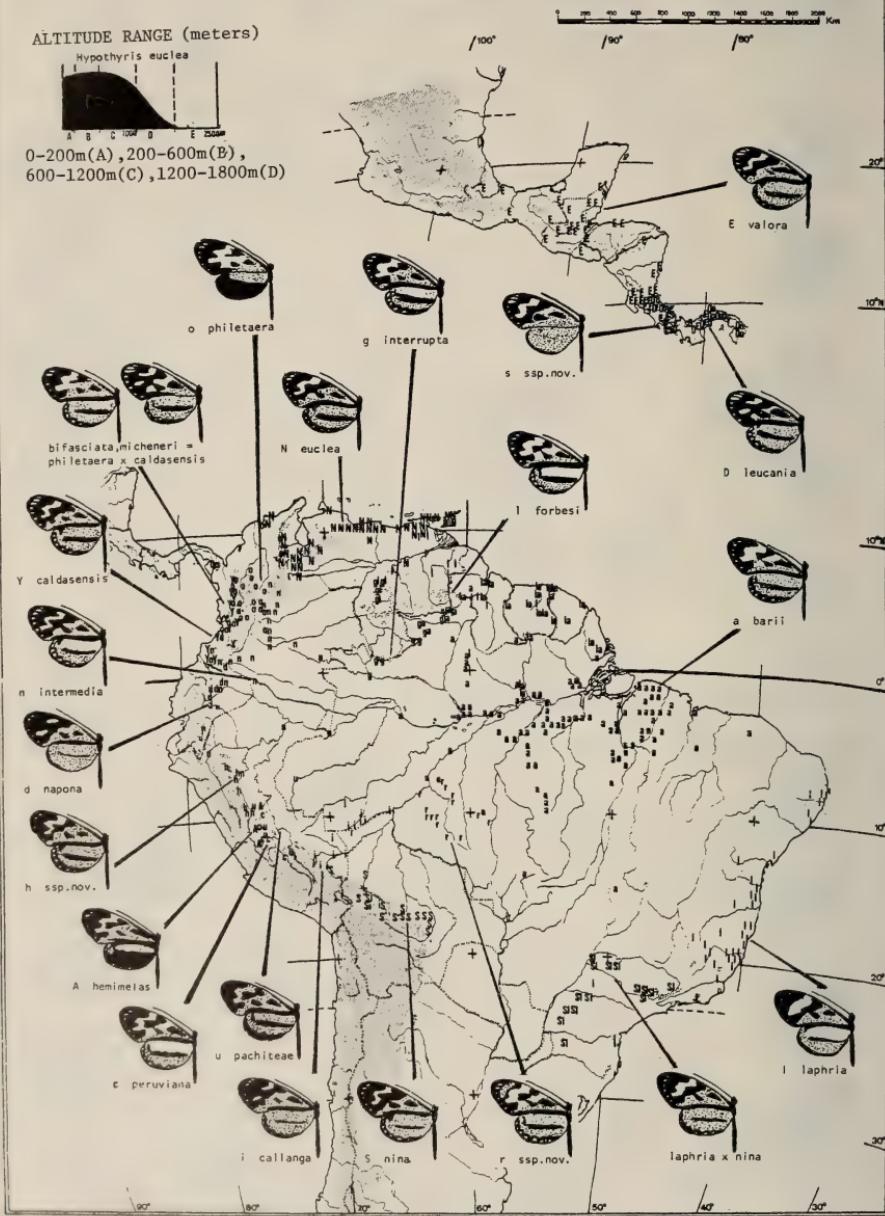
FIGURE 11
Subspecies of Hypothyris lycaste & H. anastasia
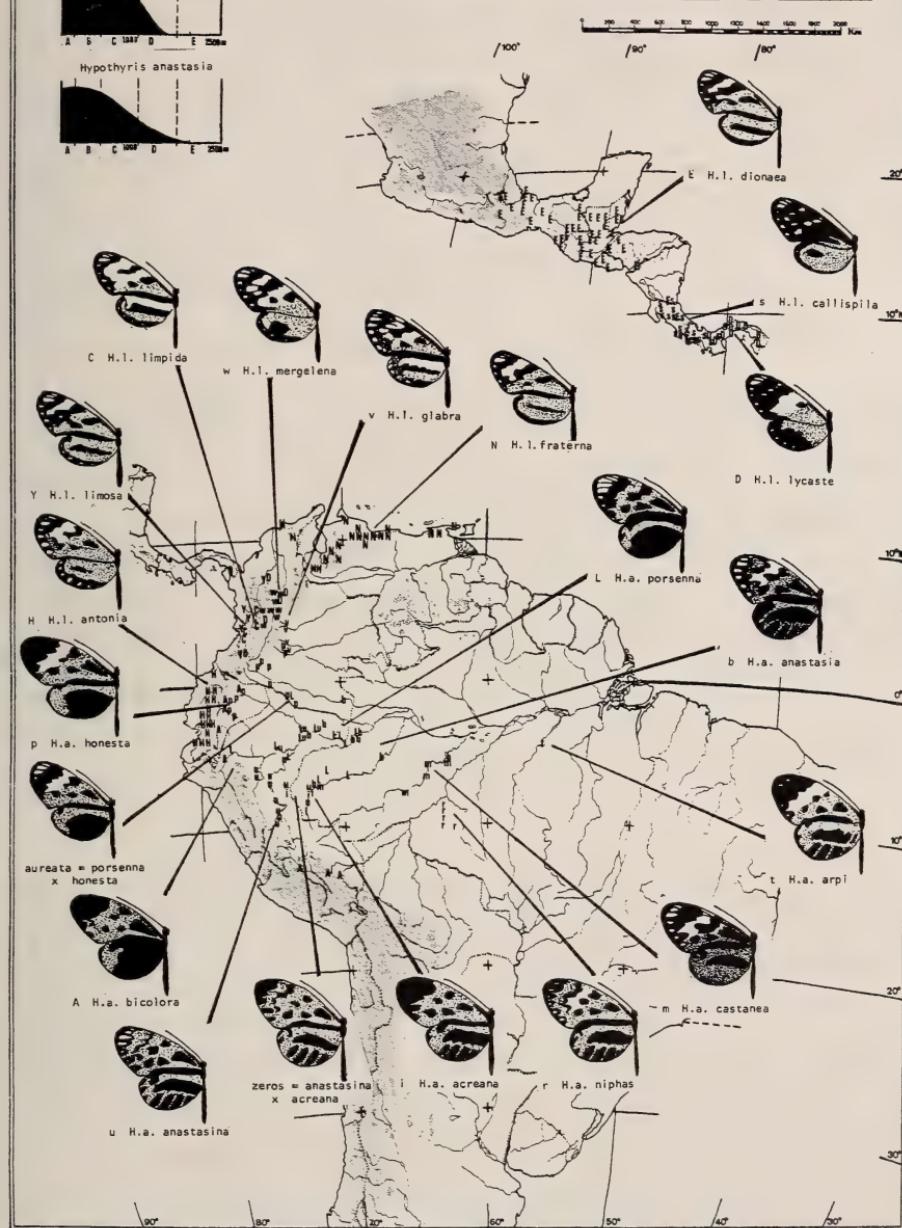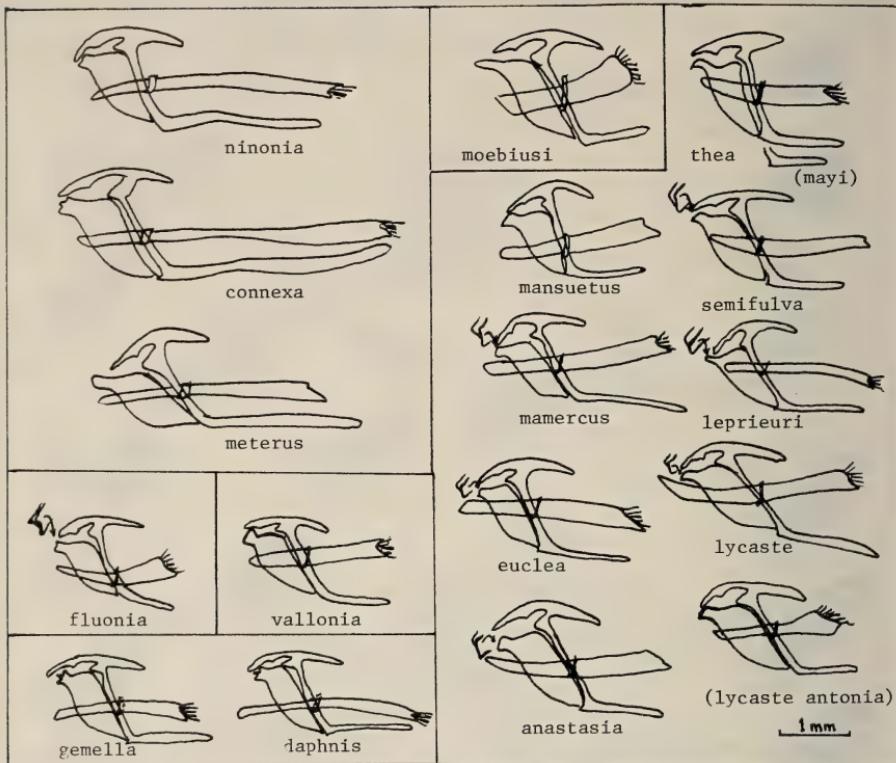
Fig. 12. Male genital armatures of *Hypothyris* species, right side, with details of valve tip (from above) when important; schematic.

areas predicted by geoscientific evidence to represent regions of high probability for longterm forest stability through the major climatic variations of the late Pleistocene (Fig. 14), all but 10 corresponded to regional subspeciation patterns in a majority of local sets of the 123 species (and 867 subspecies) of Heliconiini and Ithomiinae analyzed (Brown, 1979: 146B). Of the 44 major endemic centers recognized for this set of butterfly subspecies, 38 could be seen in those of the genus *Hypothyris* (Appendix). It is hoped that this "palaeoecological forest refuge model" (Fig. 14) may be evaluated by the examination of regional subspeciation patterns in a variety of groups of Neotropical forest Lepidoptera. Most of the centers of endemism detected in the Heliconiini and Ithomiinae (which correlate well with the regions of high probability for stability in the geoscientific model) have also been seen in a variety of other sedentary forest butterfly groups ex-

amined at the level of regional subspecies (Morphinae, Brassolini, *Phyciodes sensu lato*, Callicorini, Charaxinae, Troidini, Dismorphiinae, and a variety of Lycaenidae and Hesperioidea), as the model would predict. Note, however, that the model does not relate to species biogeography (since many butterfly species pre-date the Pleistocene), nor to local species diversity (which is usually determined by parameters of the physical environment that set a limit on packing of the species potentially present). Indeed, many of the subspecies hybridization quadrants (black in Fig. 13) show exceptionally high species diversity, and are often the source of many dispersive and weedy "commercial" Lepidoptera.

SUBSPECIES AND BIOLOGY OF *HYPOTHYRIS DAPHNIS*

By far the least known species in the genus *Hypothyris* is *H. daphnis* D'Almeida (Figs. 6, 15–21). Two of the subspecies, *H. d. daphnis* and *H. d. daphnoides*, were described only recently (1945). Three additional subspecies have come to light in the past six years, extending the continuous range of this characteristic species to the limits of the Amazon forest in Brazil, east of the basins of the Rios Madeira and Cuminá. The early stages of one of these new subspecies were observed in central Amapá in mid-1978, and are described briefly here. The three new subspecies also are described. Material is distributed to museums in which *H. daphnis* is poorly or not represented.

→

FIG. 13. Centers of butterfly subspecies endemism in the Neotropical forests (Brown, 1979, 1980), based on 3500 localities, 1520 quadrants (of 30′ × 30′ latitude and longitude), and quadrant lists for 123 species and 867 subspecies of forest Heliconiini and Ithomiinae (including all the *Hypothyris*). A double correction is applied for hybridization of subspecies or mixing of semispecies; blacked-in quadrants have negative endemism values for all endemic centers represented in their lists (i.e., more than half of the the subspecies recorded and associated with any one center are present in populations hybridized with equivalent or conspecific taxa from other centers). Single crosshatching indicates endemism values above ⅓; double crosshatching indicates values over ⅔ of the corrected maximum for the center. (This maximum value is given after the name of each center; the number which follows in parentheses is the maximum if no correction for hybridization is applied.)

FIG. 14. Regions of high probability for the continuity of humid tropical forest during the long cold, dry spell which terminated the Würm-Wisconsin glaciation, 13,000—20,000 years ago (Brown, 1979, 1980). Areas were determined by a summation of separate data sets from paleoclimatological, pedological (soil characters), geomorphological (surface landforms), and vegetational analyses, including subtraction for especially unfavorable soils and vegetation types and a double positive value for especially favorable soils.

FIGURE 13: Centers of subspecies endemism in Neotropical forest butterflies (1980)

AMERICA TROPICAL
K8 - ZOOLOGIA - UNICAMP   1979

COLOMBIA & ECUADOR

(Ne) Nechí 13(23)
(Cc) Chocó 12(18)
(Ca) Cauca 9(13)
(Mg) Magdalena 4(11)
(SM) Santa Marta 6(6)
(V) Villavicencio 17(25)
(Pt) Putumayo 10(20)
- - - - - - - - - - - - - -
(Cb) Chimborazo 24(24)
(Ab) Abitagua 12(22)
(Su) Sucúa 14(18)
(Np) Napo 7(21)

VENEZUELA/T & T

(Ct) Catatumbo 7(9)
(RG) Rancho Grande 19(20)
(ST) Sucre/Trinidad 10(10)
(Ap) Apure 10(10)

CENTRAL AMERICA

(Gt) Guatemala 19(19)
  1 Veracruz 18
  2 Tuxtlas 14
  3 Guerrero 8
  4 Pacifico 14
  5 Verapaz 19
(Ch) Chiriquí 18(24)
(Da) Darién 10(11)

GUIANA SHIELD

(It) Imataca 5(9)
(Pn) Pantepui 8(8)
(Rr) Roraima 6(8)
(Ve) Ventuari 3(3)
(Ir) Imeri 11(13)
  1 Vaupés 8
  2 Neblina 11

(MG) Manaus/ Guiana 8(21)

(JT Jari-Trombetas 8)

(Oy) Oyapock 18(22)

SOUTHERN ANDES

(Mn) Marañón 9(10)
(H) Huallaga 13(18)
(U) Ucayali 14(26)
(C) Chanchamayo 11(19)
(In) Inambari 10(19)
(Y) Yungas 19(25)
  1 La Paz 19
  2 Cochabamba 19

UPPER AMAZON BASIN

(Lo) Loreto 9(13)
(Tf) Tefé 5(12)
(Gp) Guaporé 6(10)

LOWER AMAZON

(Be) Belém 14(15)
(Ba) Marajó 5(7)
(Mj) Marajó 5(7)
(Tp) Tapajós 22(26)
(Ro) Rondônia 16(25)
(Md) Madeira 5(7)

SOUTHERN BRAZIL

(Pe) Pernambuco 6(6)
(Ar) Araguaia 7(7)
(Ba) Bahia 8(10)
(RJ) Rio de Janeiro 12(13)

Andes (8)

>1500m

FIGURE 14: Paleoecological Forest Refuges

SUGGESTED NAMES

AMERICA TROPICAL

KB - ZOOLOGIA - UNICAMP 1979

6 Nechí
7 Chocó
8 Chimborazo
9 Cauca
10 Magdalena
11 Santa Marta
12 Catatumbo
13 Rancho Grande
14 Sucre-Trinidad
15 Apure
16 Villavicencio
17 Putumayo
18 Napo
19 Abitagua-Baeza

29 Imataca
30 Cuchivero
31 Mucajaí-Catrimani
32 Parima
33 Huachamacari
34 Araçã
35 Neblina
36 São Gabriel
37 Vaupés
38 Apaporis
39 Guiana
40 Suriname
41 Oyapock
42 Serra do Navio

1 Guatemala (incl. Veracruz, Lacandona, Honduras)
2 Pacifico (incl. Guerrero, Soconusco, El Salvador)
3 Chiriquí-Azuero
4 San Blas
5 Tacarcuna

60% PROBABILITY
80-100% PROBABILITY

43 Jari-Trombetas
44 Manaus
45 Capim-Gurupi
46 Carajás
47 Tapajós-Xingú
48 Rondônia-Aripuanã
49 Purús
50 Juruá
51 Loreto-Japurá

20 Sucua
21 Marañón
22 Huallaga-Pachitea
23 Serra do Divisor
24 Chanchamayo
25 Inambari
26 Yungas
27 Uopiane
28 Guaporé

52 Ibiapaba
53 Caríris-Araripe
54 Pernambuco
55 Bahia
56 Agreste
57 Goiás
58 Pardo-Paraná
59 Paranapanema
60 Iguaçu
61 Alegre
62 Rio de Janeiro

>1500 m

0 200 400 600 800 1000 1200 1400 1600 1800 2000 Km
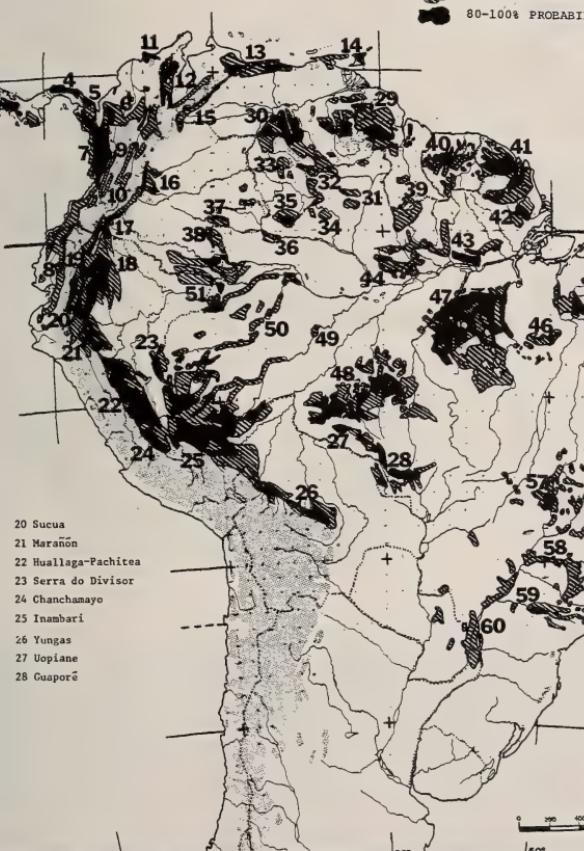
H. daphnis shows a characteristic pattern of distribution and abundance, in relation to the endemic centers (Fig. 13). The species appears uncommonly in restricted localities between the nuclei (regions with highest values for endemism) and the peripheries (regions where endemism values are positive but fall below 50% of the maximum) (Fig. 6). This suggests a partial marginalization process for the species, similar to but less accentuated than that in *H. leprieuri* (Fig. 8), which almost always occurs at the peripheries of endemic centers (endemism values near to 0). This distribution would maintain strong isolation between the subspecies of *daphnis*, but allow extensive hybridization in the subspecies of *leprieuri*.

The relationship of *H. daphnis* to *H. gemella* remains unresolved until more biological information is available. They are similar but not identical in male genitalia (Fig. 12); allopatric (Fig. 6); but they are not closely homologous in color-pattern elements. Together, they form a well-segregated subgroup within the genus *Hypothyris*.

Further discussion of speciation patterns in the genus *Hypothyris* and the biological distribution patterns of *H. leprieuri* and other species, as well as description of the many other new subspecies, must await additional fieldwork. Meanwhile, it is hoped that the species concepts presented here may be further tested in the field and in the laboratory, so that the genus may be better understood.

Hypothyris daphnis

Diagnosis. A *Hypothyris* characterized externally by the presence of a highly elongated submarginal spot in forewing space R_5-M_1, contrasting with a small rounded spot directly above it in space R_4-R_5; and internally by male genitalia with a long thick penis and a fairly short and much narrower saccus, and three distinct teeth external to the tip of the valve. Sexes similar, with females having a larger wingspan, more rounded and opaque wings, and no hair-brush on the hindwing costa. Dorsal and ventral wing surfaces similar; abdomen yellow ventrally. Distributed in Brazil, from Amapá to Ron-

$\rightarrow$

FIGS. 15–21. *Hypothyris daphnis* adults (life size; dorsal left, ventral right; black, yellow and orange) and juveniles. **15**, *H. d. daphnis*, ♂ (**a**, upper) and ♀ (**b**, lower), Jaru, Rondônia (photos courtesy of Lee D. and Jacqueline Y. Miller of the Allyn Museum of Entomology); **16**, *H. d. daphnoides* ♂, km 185 Altamira a Itaituba, Pará, 13 Oct. 1977 (K. Brown); **17**, *H. d. madeira* nov., holotype ♂ (**a**, upper) and paratype ♀ (**b**, lower), km 519 Manaus-Porto Velho highway, Amazonas, Brazil, 17 Oct. 1978 (K. Brown); **18**, *H. d. clenchi* nov., holotype ♂ (**a**, upper) and allotype ♀ (**b**, lower), 27 km NE of Marabá, Pará, 8 Oct. 1977 (K. Brown). **19**, *H. d. amapaensis* nov., holotype ♂ (**a**, upper), allotype ♀ (**b**, center), and paratype ♂ with lighter forewing and darker hindwing (**c**, lower), Lourenço, Amapá, 30 June 1978 (K. Brown); **20**, *H. d. amapaensis*, mature larva, 2×, Lourenço, Amapá, green, whitish and ochre yellow; **21**, same, pupa, 3×, brown with reflections. Scale marks at left of figure indicate cm.

15

18

16

17

19

20

21

dônia; apparently absent west of the Rio Cuminá (Paru do Oeste, Erepecuru), north of the Solimões/Amazonas (where replaced by the congener *H. gemella*), and in the upper Amazon (where not substituted by any close species).

Key to subspecies

1a. Forewing median yellow patch broad, continuous from costal to anal margin, with postmedian yellow band narrow, broken into separate spots **2**

1b. Forewing median and postmedian yellow bands nearly equal in width, separated by an irregular undulate black band **3**

2a. Hindwing median black band narrow, margin with large yellow spots .... *d. daphnoides*

2b. Hindwing median band broad or fused with all-dark margin *d. amapaensis* nov.

3a. Hindwing median band broken into four widely separated spots *d. madeira* nov.

3b. Hindwing median black band essentially continuous **4**

4a. Forewing median black band jagged, postmedian yellow band narrow, often discontinuous; hindwing orange above a jagged black median band, with prominent yellow spots in the dark marginal area .... *d. daphnis*

4b. Forewing postmedian black band smoother, postmedian yellow band broad and continuous; hindwing orange above a smooth narrow median black band, no prominent yellow spots in narrow marginal black .... *d. clenchi* nov.

The distributions of the subspecies are shown in Fig. 6; all are illustrated in Figs. 15–19. Description of the three new subspecies follows notes on the two described previously by D'Almeida (1945).

Hypothyris daphnis daphnis D'Almeida, 1945
(Figs. 6 & 15)

Forewing (24–27 mm) with a jagged black band dividing the median-postmedian yellow region into two discontinuous crossbands of nearly equal width. **Hindwing** median black bar jagged but continuous; orange costally of this; marginal black including large yellow spots.

Distribution. Northwestern Mato Grosso, extreme southern Amazonas, most of Rondônia to extreme northern Bolivia (Guayeramerin). Registered localities and coordinates:

Cidade Humboldt, Rio Aripuanã, Mato Grosso (10°13′S, 59°22′W)
Mina Igarapé Preto, Amazonas (8°34′S, 61°10′W)
Cachoeira do Samuel, Rio Jamari, Rondônia (8°45′S, 63°27′W)
Rio Jamari, Rondônia (southwest of 9°S, 63°W)
Porto Velho, Rio Madeira, Rondônia (8°45′S, 63°53′W)
São Carlos, Rio Madeira, Rondônia (9°05′S, 64°05′W)
44 km N of Ariquemes, Rondônia (9°35′S, 63°03′W)
26 km SW of Ariquemes, Rondônia (10°04′S, 63°13′W)
Porto Velho to Vilhena, km 260, Rondônia (10°18′S, 62°39′W)
Jaru, Rondônia (10°27′S, 62°27′W)—very abundant in region
Riozinho, Rondônia (11°30′S, 61°20′W)
Jiparaná (Vila de Rondônia), Rondônia (10°52′S, 61°57′W)
Guajara-Mirim/Guayeramerin, Rio Madeira, Rondônia/Bolivia (10°47′S, 65°20′W)

Hypothyris daphnis daphnoides D'Almeida, 1945
(Figs. 6 & 16)

Forewing (24–27 mm) crossed by a broad continuous yellow median patch and a narrow, broken postmedian spot-band. **Hindwing** black median band jagged, margin with large yellow spots.

Distribution. Area between the Xingu and Tapajós Rivers, Pará, Brazil, principally between 3° and 5° south latitude. Registered localities and coordinates:

22 km W of Belo Monte, Rio Xingu, Pará (Rodovia Transamazônica) (3°05′S, 51°52′W)
Brasil Novo, km 35, Altamira a Itaituba, Pará (Rodovia Transmazônica) (3°18′S, 52°33′W)
km 100, Altamira a Itaituba, Pará (3°29′S, 53°01′W)
km 124, Altamira a Itaituba, Pará (3°32′S, 53°11′W)
km 162, Altamira a Itaituba, Pará (3°39′S, 53°29′W)
km 185, Altamira a Itaituba, Pará (3°43′S, 53°44′W)
Rurópolis Presidente Médici, km 1552 Cuiabá-Santarém (junction with Rodovia Transamazônica), Pará (4°04′S, 54°56′W)
Igarapé Tinga, km 1557 Cuiabá-Santarém, Pará (4°01′S, 54°58′W)
km 190, Santarém a Rurópolis (km 1578 Cuiabá-Santarém), Pará (3°53′S, 54°54′W)
Monte Cristo, Rio Tapajós, Pará (4°05′S, 55°38′W)

Hypothyris daphnis madeira Brown new subspecies
(Figs. 6 & 17)

Forewing 25–29 mm (large for the species). Similar on the forewing to *H. d. daphnis*, but with the median black band smoothed to form a near-interrupted sinuate spot-band and a subtriangular cubital spot; black cell-spot large, rounded. **Hindwing** median black bar broken up into four separate oval spots.

Types: HOLOTYPE ♂, km 519 Manaus-Porto Velho highway, Amazonas, Brazil, ravine to west of road (6°31′S, 62°54′W), 17 Sept. 1978 (K. Brown), deposited in the Museu Nacional (Rio de Janeiro). ALLOTYPE ♀, Lago Acará, Rio Madeira, Amazonas, Brazil (southwest of 6°S, 62°W), Museu Nacional (Rio de Janeiro). One ♂ and 15 ♀ PARATYPES, same data as holotype; ♀ paratype distributed to each of the Museu Nacional (Rio de Janeiro), Departmento de Zoologia da Universidade Federal do Paraná (Curitiba), Museu Goeldi (Belém), Instituto Nacional de Pesquisas da Amazônia (Manaus), Allyn Museum of Entomology (Sarasota), American Museum of Natural History, National Museum of Natural History, Cornell University Collection, Carnegie Museum (Pittsburgh), Museum National d'Histoire Naturelle (Paris), Museum für Naturkunde (Berlin), and Zoologisches Sammlung des Bayerischen Staates (Munich); ♂ and 3 ♀ retained in author's collection. 3 ♂ and 5 ♀ PARATYPES, same data as holotype except collected by D. Gifford; one pair deposited in the British Museum (Natural History), ♀ in the Royal Scottish Museum (Edinburgh), 2 ♂ and 3 ♀ retained by D. Gifford, Brasilia. One ♀ PARATYPE, "amont (below) Manaus," from Stoffel collection *via* H. Descimon, collection of the author.

Hypothyris daphnis clenchi Brown new subspecies
(Figs. 6 & 18)

Forewing (24–27 mm) not so heavily nor jaggedly marked with black as in *H. d. daphnis*, with a continuous and broad yellow postmedian band reducing the apical black area. **Hindwing** with median band smooth and narrow; marginal black also narrow with no yellow spots; disc translucent yellow in both sexes.

Types. HOLOTYPE ♂, 27 km NE of Marabá on highway PA-070, Pará, Brazil (5°11′S, 48°57′W), 8 Oct. 1977 (K. Brown), deposited in the Museu Nacional (Rio de Janeiro). ALLOTYPE ♀, Fazenda Terrasse, km 108, Açailândia-Santa Luzia road, Maranhão (4°24′S, 46°44′W), 2 Aug. 1974 (O. Mielke), in the Departamento de Zoologia, Universidade Federal do Paraná (Curitiba). 2 PARATYPE ♂, same data as holotype, retained in the author's collection. PARATYPE ♀, same data as allotype except 3 Aug. 1974, in the same collection (DZ-UFP). PARATYPE ♀, Água Azul, km 1490 Belém-Brasília highway, Município Paragominas, Pará, Brazil (4°20′S, 47°32′W), 16 Aug. 1974 (O. Mielke), also in the DZ-UFP. PARATYPE ♀, 33 km W of Paragominas (23 km E of large bend of the Rio Capim towards the west), Município de Paragominas, Pará

(2°58′S, 47°38′W), 5 Oct. 1977 (K. Brown), deposited in the Museu Goeldi (Belém). PARATYPE ♀, 30 km N of Marabá, Pará on PA-050 (5°03′S, 49°03′W), 8 Oct. 1977 (K. Brown), deposited in the British Museum (Natural History).

Hypothyris daphnis amapaensis Brown **new subspecies**
(Figs. 6 & 19)

Forewing (23–26 mm) similar to *H. d. daphnoides*, with a broad yellow median patch and four small postmedian spots. **Hindwing** much darker, the marginal black area without light spots, and the black median band heavy, occasionally fused to the marginal black.

Types. HOLOTYPE ♂ and ALLOTYPE ♀, Lourenço (Mines), Amapá, Brazil (2°19′N, 51°38′W), 29 June 1978 (K. Brown), donated to the Museu Nacional, Rio de Janeiro. 7 ♂ and 15 ♀ PARATYPES, same locality, 27 June to 1 July 1978 (K. Brown); one pair in each of the Museu Goeldi (Belém), the British Museum (Natural History), the American Museum of Natural History, and the Allyn Museum (Sarasota); ♀ in each of the Museu Nacional (Rio de Janeiro), Instituto Nacional de Pesquisas da Amazônia (Manaus), Departamento de Zoologia da Universidade Federal do Paraná (Curitiba), National Museum of Natural History (Washington), Cornell University collection (Ithaca), Carnegie Museum (Pittsburgh), Museum National d'Histoire Naturelle (Paris), Museum für Naturkunde (Berlin), and Zoologisches Sammlung des Bayerischen Staates (Munich); 3 ♂ and 2 ♀ retained in the author's collection. 3 ♀ PARATYPES, Utu, km 75 Calçoene-Lourenço, Amapá, Brazil (2°27′N, 51°24′W), 25–26 June 1978 (K. Brown), in the author's collection. ♀ PARATYPE, no locality (probably near Calçoene, Amapá), in the Museu Goeldi, Belém. ♂ PARATYPE, Tiriós, upper Rio Paru do Oeste (=Cuminá), Pará, Brazil (2°14′N, 55°57′W), 29 Jan. 1975 (P. Bührnheim), in the author's collection.

Juvenile stages of *Hypothyris daphnis amapaensis*

During work in Lourenço, Amapá, in June 1978, I had occasion to observe two females of *H. daphnis amapaensis* ovipositing on plants of *Solanum asperum* L.-Cl. Rich.; one was a small bush on a field-and-stream edge (a typical habitat, where this plant is heavily attacked by *Hypothyris euclea* all over tropical Brazil), the other was a small tree in the middle of very dense forest above a small stream. A number of eggs and larvae in various stages were collected from these two plants. The larger larvae were reared to adults on the leaves of *S. asperum*, giving one male and one female (not paratypes). A brief summary of the early stages follows:

Egg subspherical (flattened where attached to leaf), glistening white, 0.5 mm in diameter, with numerous horizontal and vertical ridges, much as in the eggs of other solitary *Hypothyris* and many other Ithomiinae.

Larva (hatching after at least four days) initially translucent yellow, changing to greenish after feeding. First three instars (two to three days each) with few distinguishing marks other than the usual development of a "corrugated effect." They progress from rasping the underside of leaves to chewing at the edges.

Fourth instar larva similar to the fifth (Fig. 20). Mature larva near 30 mm in length; dorsally gray-green, supralaterally strong ochre yellow in a wide band. Semicircular lateral projections, one per segment, on the thorax and abdomen; each segment divided unequally in five "corrugations." Head and anal segment light greenish-white.

Total duration of larval feeding stage was about two weeks.

Prepupa doubled over in a "U" loop; whitish to yellowish. Duration one day.

Pupa (Fig. 21) brown, with some weak reflectiveness on wing-cases; strongly bowed

to assume the typical humped shape of many ithomiine pupae; eyes projecting in cones; wing cases and abdomen spotted with darker brown. Not nearly as silvered as most Dircennine pupae, but very similar to *Hypothyris ninonia*, *H. euclea*, and other *Hypothyris* pupae in shape and coloration. Duration eight days.

Adults emerge in the early morning, and fly before midday. They may then be found sparingly in the heavy, humid forest in steep ravines of the Serra Lombard around Lourenço Mines, where they fly all day long and are readily attracted to *Heliotropium* bait.

ACKNOWLEDGMENTS

LITERATURE CITED

BROWN, K. S., JR. 1977. Centros de evolução, refúgios quaternários e conservação de patrimônios genéticos na região neotropical: padrões de diferenciação em Ithomiinae (Lepidoptera: Nymphalidae). Acta Amazonica 7: 75–137.

——— 1979. Ecologia Geográfica e Evolução nas Florestas Neotropicais. Universidade Estadual de Campinas, Campinas, São Paulo. 2 vols. xxxi + 265 + 120 p.

——— 1980. Paleoecology and regional patterns of evolution in neotropical forest butterflies. *In* G. T. Prance (Ed.), The Biological Model for Diversification in the Tropics. Columbia University Press, New York. in press.

D'ALMEIDA, R. FERREIRA. 1945. Novos Ithomiidae da fauna brasileira. (Lepidoptera, Rhopalocera). Bol. Mus. Nac. Rio de Janeiro, N.S., Zoologia 39: 1–13, 3 pl.

FOX, R. M. & H. G. REAL. 1971. A Monograph of the Ithomiidae (Lepidoptera). Part IV. The Tribe Napeogenini Fox. Mem. Amer. entomol. Inst. 15: i–vi, 1–368.

MIELKE, O. H. H. & K. S. BROWN, JR. 1979. Suplemento ao Catálogo dos Ithomiidae Americanos de R. Ferreira D'Almeida (Lepidoptera) (Nymphalidae: Ithomiinae). Universidade Federal do Paraná, Curitiba, Paraná. vii + 216 p.

APPENDIX

Speciation and subspeciation in *Hypothyris* (Ithomiinae: Napeogenini)

The fundamental organization of the genus *Hypothyris*, based principally on male genitalia as employed in Fox & Real (1971), needs very little change. Fieldwork in hybridization zones has produced some unexpected indications of conspecificity of taxa maintained separate in that revision. A survey of the genitalia of most of the members

of the genus (Fig. 12) also led to some surprises; not only did the genital armatures show appreciable variation within externally homogeneous populations, but also appreciably different genitalia were seen in patently conspecific taxa. For this reason, a biogeographical component was included along with the morphological parameters in the laying out of polytypic species (Figs. 2–11). Biological information from natural hybrid zones was employed whenever available; for example, it supported conspecificity of *H. vallina* and *H. pellucida* with *H. ninonia*, of *H. hygia* and *H. rowena* with *H. fluonia*, of *H. "aemilia"* and *H. fulminans* with *H. semifulva*, of *H. pyrippe* with *H. mamercus*, of *H. philetaera* and *H. laphria* with *H. euclea*, and of *H. honesta* with *H. anastasia*. Some of these unions were also supported by the biology of juvenile forms. In other cases, biological data confirmed the incompatibility of closely related species of similar morphology, such as *H. connexa* and *H. ninonia*, or *H. lycaste* and *H. anastasia*. Wide sympatry and strongly variant morphology suggested separate species status in the cases of *mansuetus* and *moebiusi*, *leprieuri* and *euclea*, and *vallonia* and *fluonia*. Many other decisions were educated guesses, based on a combination of morphology, biology, biogeography, and homology of minor color-pattern characters; for example, there is as yet no compelling biosystematic evidence for the association of *H. daeta* and *H. fimbria* with *H. ninonia* (although *diphes* seems secure there), of the Amazonian and Andean groups of subspecies of *H. mamercus* with each other, of *H. mayi* with *H. thea*, or of *H. glabra* with *H. lycaste*. The genitalia of *H. lycaste antonia* (Fig. 12) are very deviant within this species, and it may not be interfertile with *H. l. limosa*, though a recent common ancestry for the two seems very likely.

Examination of the respective types revealed that *Hypothyris glabra carvalhoi* (*sensu* Fox & Real) is in fact a subspecies of *Rhodussa cantobrica*, as originally described by D'Almeida. The very yellow, but ventrally orange-washed *ninonia* from north of the Roraima area (in Bolivar, Venezuela—Imataca center, Fig. 13) corresponds to *mysotis* (Haensch), differing from *colophonia* D'Almeida from south of Roraima in Brazil, and "*pellucida*," "*vallina*," and "*colosseros*" are transitions between these and neighboring subspecies (see Fig. 2). *Napeogenes seminigra* is in fact a subspecies of *Hypothyris fluonia* (and an older name for "*satterwhitei*" Fox & Real), as is the "problematic" *H. manaos*. *Maenas* is actually a transition between the extreme melanic phenotype illustrated by Fox & Real (1971) and a new subspecies from lower elevations (Fig. 9); for the sake of stability this name should be applied to all orange-and-black populations from higher elevations in the Peruvian Andes. Weymer's *nemea* is an older name for Real's "*surinamensis*," but "*neustetteri*" and its senior synonym "*bifasciata*" are intergrades between *H. euclea philetaera* and *H. e. caldasensis*. The correct name for the Pernambuco subspecies of *H. ninonia* is *evanescens* Haensch or, if the original description be impugned for mistaken reference to an earlier name, is *evanescens* D'Almeida, 1923 (as a form) or 1939. Weymer's *daetina*, a dark chocolate form, must remain a *species inquerendum* until it is recaptured in Bahia. The oldest name for Riley's *medea* is *castanea* Butler (the male lectotype as designated by Mielke & Brown, 1979: 90, not the female illustrated by Butler = *a. anastasia*). The holotype designated by Haensch for his *latefasciata* is a senior synonym of *fugitiva* Fox, while Feisthamel's *leprieuri* (used with an extra "i" by Fox & Real for the Oyapock subspecies of *H. ninonia* = *H. n. latefasciata*) is actually the oldest named subspecies of the complex represented elsewhere by *ignorata*, *michaelisi*, *catilla*, *ninyas*, and a host of new subspecies (Fig. 8).

H. semifulva has two month's priority over "*aemilia*" for the species including both, which is fortunate because the latter name represents a rare transitional form between *H. s. angelina* and *H. s. pallisteri*.

The types of essentially all names have been seen. The majority of geographical subspecies recognized here (marked with an asterisk in Fig. 1) were studied in monomorphic populations in the field, in the appropriate regions. Names marked with a dagger on the list below were dissected to verify male genitalia, or slides prepared by Fox or Godman were examined in collections in the National Museum of Natural History or the British Museum, respectively.

Most specimens should be able to be rapidly identified with the drawings and geographical ranges shown in Figs. 2–11. In cases of doubt, the genitalia can be compared with those schematized in Fig. 12. The taxa which are most often confused on superficial characters are *ninonia/connexa* and *gemella/vollonia* in the Pantepui area, some *thea/leprieuri* (note the different shape of the FW yellow median band, especially the distal border), *meterus/semifulva/anastasia* in the high Andes (genitalia work best), *ninonia/euclea/mamercus* in parts of the Amazon (the long narrow penis of the first can often be directly observed without a lens or dissection), *semifulva/mansuetus* in central Peruvian valleys (note the distal border of the FW yellow band), *leprieuri/euclea/ninonia* in various parts of the Amazon (compare the FW yellow fascia carefully), and *anastasia* with like species in the upper Amazon (the disjunct comma-mark in FW space Cu_1–Cu_2 will identify all *anastasia* subspecies).

At least ten, perhaps twenty more subspecies of *Hypothyris* should appear with intensive work in still little-explored parts of the Neotropics (in addition to the 31 already identified and still undescribed). Several of these, especially from the Marajó and Ventuari regions, are already in hand but awaiting broader field data and longer series to help decide on their status.

A list of the recognized specific and subspecific taxa follows, along with the association of each with an endemic center (Fig. 13) as used in the quantitative analysis of corrected endemism (Brown, 1979, 1980).

Genus HYPOTHYRIS Hübner, 1821

ninonia (see Fig. 2)
†*granadensis* (Haensch, 1905)   Magdalena(?)
†*fimbria* (Hewitson, 1855)   Villavicencio
diphes Fox, 1971   Putumayo
†*latipennis* (Tessmann, 1928)
   (*antonina* Staudinger =
   latipennis × *apollinis*)   Ucayali
†manuscript subspecies
   (Brown)   Inambari
aetha Fox & Real, 1971   Yungas
†*cornelie* (Guérin-
   Méneville, 1844)   Guaporé
†*mysotis* (Haensch, 1909)   Imataca
†*colophonia* D'Almeida, 1945   Roraima
†manuscript subspecies
   (Brown)   Pantepui
†*completomaculata* (Zikán,
   1941)   Imerí
†*mutilla* (Hewitson, 1867)   Guiana
†*completa* (Haensch, 1905)   Manaus
†*latefasciata* (Haensch, 1905)   Oyapock
†*ninonia* (Hübner, 1806)   Belém
†manuscript subspecies
   (Brown)   Tapajós
†*neimyi* (Riley, 1931)   Rondônia
manuscript subspecies
   (Brown)   Madeira
manuscript subspecies
   (Brown)   Tefé
†*apollinis* (Staudinger, 1884)   Loreto
†*evanescens* (Haensch, 1909)   Pernambuco
†*daeta* (Boisduval, 1836)   Rio de Janeiro
meterus (see Fig. 3)
zephyrus Fox, 1945   Putumayo
†*meterus* (Hewitson, 1860)   Andes
deemae Fox, 1943   Chanchamayo
†manuscript subspecies
   (Lamas)   Inambari
connexa (see Fig. 3)
†*lema* Brown, 1977   Imataca
†*connexa* (Hall, 1939)   Pantepui
†manuscript subspecies
   (Brown)   Imerí

gemella (see Fig. 6)
†*gemella* Fox, 1971   Imataca
†manuscript subspecies
   (Brown)   Pantepui
†manuscript subspecies
   (Brown)   Roraima
daphnis (see Fig. 6)
amapaensis Brown, 1980   Oyapock
clenchi Brown, 1980   Belém
†*daphnoides* D'Almeida, 1945   Tapajós
†*daphnis* D'Almeida, 1945   Rondônia
madeira Brown, 1980   Madeira
fluonia (see Fig. 4)
†manuscript subspecies
   (Brown)   Apure
†*rowena* (Hewitson, 1857)   Villavicencio
berna (Haensch, 1903)   Napo
uchiza Lamas, 1979   Huallaga
†*pardalina* (Hopffer, 1874)   Ucayali
seminigra (Rosenberg &
   Talbot, 1914)   Inambari
†*viola* (Haensch, 1905)   Yungas
†*hygia* (Godman, 1899)   Oyapock
manuscript subspecies
   (Brown)   Belém
†manuscript subspecies
   (Brown)   Tapajós
†*manaos* (Bates, 1862)   NW-Tapajós
      (Maués)
†*tiberina* D'Almeida, 1945   Rondônia
flavigera (Riley, 1919)   Madeira
fluonia (Hewitson, 1854)   Tefé
fulvifascia (Talbot, 1932)   Loreto
†*violantilla* D'Almeida, 1952   Araguaia
vallonia (see Fig. 5)
†manuscript subspecies
   (Brown)   Roraima
†*glycon* (Godman, 1899)   Manaus/
      Guiana
†*vallonia* (Hewitson, 1854)   Belém
†manuscript subspecies
   (Brown)   Tapajós

Genus HYPOTHYRIS Hübner, 1821,
continued.

semifulva (see Fig. 5)
　†fulminans (Butler, 1873)　　Villavicencio
　　putumayoensis Fox & Real,
　　　1971　　　　　　　　　　Putumayo
　†satura (Haensch, 1903)　　Napo
　†semifulva (Salvin, 1869)　　Sucúa
　†pallisteri Fox & Real, 1971　Huallaga
　†angelina (Haensch, 1905)　Napo
　†meteroides Fox, 1971　　　Andes
　　virgilini (Riley, 1919)　　Inambari
　†dalmeidai Fox & Real, 1971　Rondônia
　†soror (Srnka, 1885)　　　　Loreto
moebiusi (see Fig. 7)
　†moebiusi (Haensch, 1903)　Napo
　†manuscript subspecies
　　（Lamas）　　　　　　　Huallaga
　　unicolora (Tessmann, 1928)　Ucayali
mansuetus (see Fig. 6)
　†amica (Weymer, 1884)　　Sucúa
　　klotsi Fox, 1941　　　　　Marañón
　†mansuetus (Hewitson, 1860)　Chanchamayo
mamercus (see Fig. 9)
　　polymnides (Haensch, 1905)　Putumayo
　　mamercus (Hewitson, 1869)　Napo
　　pyrippe (Hopffer, 1874)　　Sucúa
　　manuscript subspecies
　　　（Brown）　　　　　　Huallaga
　　maenas (Haensch, 1909)　Andes
　　manuscript subspecies
　　　（Brown）　　　　　　Guaporé
　†poemne D'Almeida, 1939　Manaus
　†manuscript subspecies
　　　（Brown）　　　　　　Tapajós
　†manuscript subspecies
　　　（Brown）　　　　　　Rondônia
thea (see Fig. 3)
　　manuscript subspecies
　　　（Lamas）　　　　　　Ucayali
　　manuscript subspecies
　　　（Brown）　　　　　　Inambari
　†thea (Hewitson, 1852)　　Manaus
　†mayi D'Almeida, 1945　　Altamira
　　　　　　　　　　　　　（Tapajós—NE)
　　theatina (Haensch, 1909)　Tapajós
leprieuri (see Fig. 8)
　　manuscript subspecies
　　　（Lamas）　　　　　　Ucayali
　　manuscript subspecies
　　　（Brown）　　　　　　Inambari
　†catilla (Hewitson, 1875)　Yungas
　†manuscript subspecies
　　　（Brown）　　　　　　Guaporé
　　manuscript subspecies
　　　（Brown）　　　　　　Roraima
　　nemea (Weymer, 1899)　Guiana
　†michaelisi (Haensch, 1909)　Jari-Trombetas

　　leprieuri (Feisthamel, 1835)　Oyapock
　　manuscript subspecies
　　　（Brown）　　　　　　Belém
　　ignorata (Haensch, 1905)　Tapajós
　　manuscript subspecies
　　　（Brown）　　　　　　Cachimbo
　　　　　　　　　　　　　（Tapajós—S)
　†ninyas D'Almeida, 1945　Rondônia
　†manuscript subspecies
　　　（Brown）　　　　　　Rio de Janeiro
euclea (see Fig. 10)
　　valora (Haensch, 1909)　Guatemala
　　manuscript subspecies
　　　（Brown）　　　　　　Chiriquí
　　leucania (Bates, 1863)　Darién
　　philetaera (Hewitson, 1876)　Nechí
　　caldasensis Fox, 1971　Chocó
　　euclea (Godart, 1819)　Rancho Grande
　†intermedia (Butler, 1873)　Napo
　　napona (Haensch, 1903)　Abitagua
　　manuscript subspecies
　　　（Lamas）　　　　　　Huallaga
　　hemimelas (Staudinger,
　　　1885)　　　　　　　　Andes
　　pachiteae (Tessmann, 1928)　Ucayali
　　peruviana (Staudinger, 1885)　Chanchamayo
　†callanga (Haensch, 1905)　Inambari
　　nina (Haensch, 1905)　Yungas
　†forbesi Fox, 1941　　　　Imataca
　　interrupta (Zikán, 1941)　Imeri
　　barii (Bates, 1862)　　　Belém
　　manuscript subspecies
　　　（Lamas）　　　　　　Rondônia
　†laphria (Doubleday, 1847)　Bahia
lycaste (see Fig. 11)
　　dionaea (Hewitson, 1854)　Guatemala
　†callispila (Bates, 1866)　Chiriquí
　†lycaste (Fabricius, 1793)　Darién
　†limosa Fox, 1971　　　　Chocó
　†antonia (Hewitson, 1869)　Chimborazo
　　limpida (Haensch, 1905)　Cauca
　　mergelena (Hewitson, 1860)　Magdalena
　†fraterna (Haensch, 1909)　Rancho Grande
　†glabra (Godman, 1899)　Villavicencio
anastasia (see Fig. 11)
　†honesta (Weymer, 1884)　Putumayo
　　bicolora (Haensch, 1903)　Andes
　　anastasina (Staudinger,
　　　1885)　　　　　　　　Ucayali
　　acreana D'Almeida, 1958　Inambari
　　arpi D'Almeida, 1958　　Tapajós
　　niphas D'Almeida, 1945　Rondônia
　　castanea (Butler, 1877)　Madeira
　　anastasia (Bates, 1862)　Tefé
　†porsenna (Srnka, 1885)　Loreto

RESURRECTION OF THE GENUS *MORPHEIS* (COSSIDAE), WITH DESCRIPTION OF A NEW SPECIES IN THE *COGNATUS* GROUP FROM SOUTHERN ARIZONA

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ABSTRACT. The New World genus *Morpheis* Hübner is resurrected and distinguished from the Old World genus *Xyleutes* Hübner, with *Neocossus* Houlbert and *Xylotrypa* Turner as synonyms of *Morpheis*. A new classification is proposed for the 12 known species of *Morpheis*, of which 10 are new combinations. *Morpheis clenchi* (Santa Cruz Co., Arizona, U.S.A.) is described as new, and a key and photographs are provided for the three species in the *cognatus* group.

For more than a decade, moth collectors working in the vicinity of Peña Blanca Lake, west of Nogales, Arizona, have been finding a strikingly patterned, large cossid moth. Because of its large size and conspicuous appearance, a collector's initial response might be that he had discovered a bizarre new sphinx moth. In addition to describing that new species here, I am taking the opportunity to associate it with its previously described congeners, all 11 of which are Latin American species that have been erroneously placed, most recently, in the Old World genus *Xyleutes* Hübner, and earlier in the largely overlooked genera *Neocossus* Houlbert and *Xylotrypa* Turner.

HISTORICAL BACKGROUND

Hübner (1820: 196) erected the genus *Morpheis* for two species, *Hepialus scalaris* Fabricius (1775: 590) and *Sphinx pyracmon* Cramer (1780: 169). The former species is currently placed in the Oriental and African cossid genus *Azygophleps* Hampson (1892: 309), of which it is the type species, and the latter species was designated the type of the Neotropical genus *Morpheis* by Roepke (1957: 18), who at the same time retained *Morpheis* in the synonymy of *Xyleutes*.

In a revision of the world species of *Xyleutes*, Houlbert (1916: 89) proposed the new subgenus *Neocossus* for all but one of the American species he knew at the time; later in the same work (p. 105) he designated [*Endoxyla*] *strigillata* Felder (1874: Pl. 81, Fig. 5) as the type species. Houlbert's segregation of this subgenus was based partly on geographical distribution and on the presence of a distinctive longitudinal color stripe through the center of the forewing.

Apparently unaware of Houlbert's work, Turner (1918: 162) recognized the distinctiveness of at least one of the New World "*Xyleutes*," and, based on structural characters (palpi, tibial spurs, and venation), proposed the new genus *Xylotrypa*, with *strigillata* Felder

the type (by monotypy). *Xylotrypa* is thus a junior objective synonym of *Neocossus*, and both fall as junior subjective synonyms of *Morpheis*.

While *Morpheis* has lain in the synonymy of *Xyleutes* virtually since it was proposed, *Neocossus* and *Xylotrypa* remained overlooked or unmentioned for decades; both were omitted from *Lepidopterorum Catalogus* (Dalla Torre, 1923) and *Macrolepidoptera of the World* (Dyar & Schaus, 1937). Costa Lima (1945: 151) appears to have been the first to notice *Xylotrypa*, but treated it as a synonym of *Xyleutes*. Viette (1952: 60), in his catalog of the world genera of Cossidae, appears to have been the first to "rediscover" *Neocossus*, although he overlooked *Xylotrypa*. Roepke (1957: 18) recognized *Neocossus*, but as a synonym of *Xyleutes*, and likewise overlooked *Xylotrypa*.

Classification

As presently defined, the Zeuzerinae are easily distinguished from all other cossids, at least in the New World, by the distinctive male antennae, which are bipectinate—with long, downcurved rami—for only one-half to two-thirds the length of the shaft, and then become abruptly short uniserrate to the tip. Additionally, in members of this subfamily vein R_1 on the forewing arises from the areole, or from the discal cell very near the origin of the areole. This latter condition is not unique, however, because at least two genera of Cossinae share it (*Trigena* Dyar and *Cossula* Bailey). Both sexes of these, however, may be distinguished from the Zeuzerinae by having antennae uniformly uni- or bipectinate to the tip.

Morpheis may be distinguished from other New World zeuzerines by the following combination of characters: a contrastingly dark, broad, irregular, longitudinal stripe on the forewing, extending from the bases of the costa and discal cell, crossing the lower outer angle of the discal cell and reaching (in well-marked species) the termen at the distal end of vein R_5; few or no transverse wing markings; arolium absent; forewing with vein R_1 arising from the areole; forewing with vein M_1 arising at or very near the distal end of the chorda (the common vein dividing the areole from the discal cell); and by the prominent development of the gnathos and presence of a process on the sacculus of the male genitalia. Several American species formerly placed in *Xyleutes* (see Dyar & Schaus, 1937; Forbes, 1942) are not referable to *Morpheis*, but belong in *Psychonoctua* Grote (1866: 249) or an undescribed genus.

The type species of *Xyleutes* is the south Asian *Phalaena strix* Linnaeus (1758: 508), designated by Kirby (1897: 144), and not the
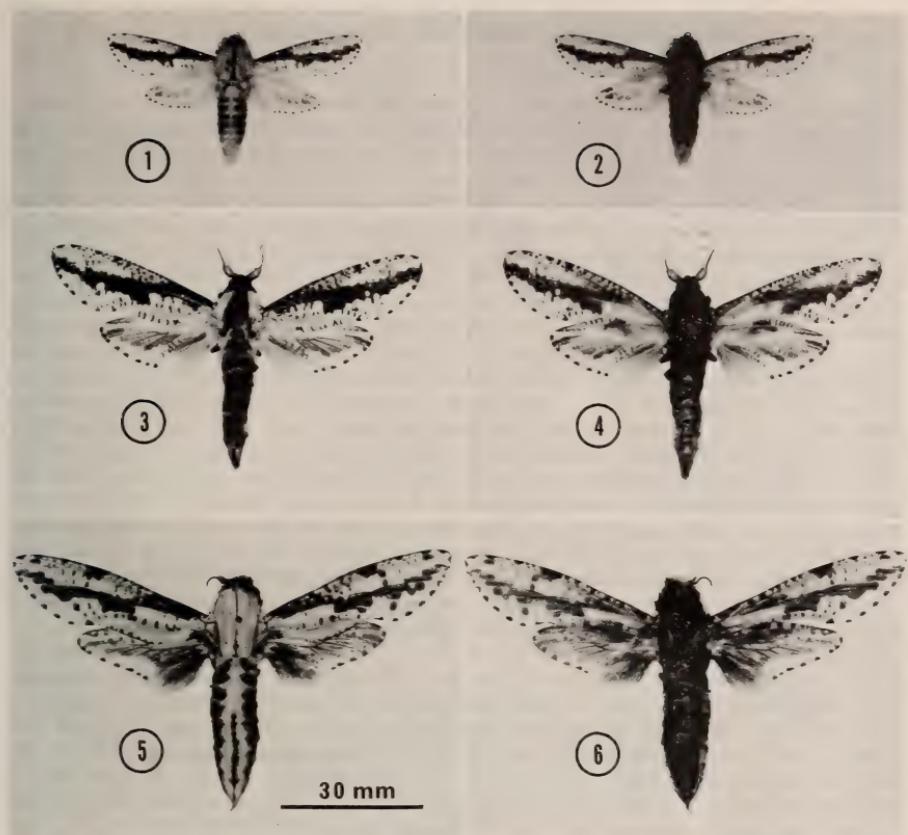
FIGS. 1–6. Adult male *Morpheis*. **1–2,** *M. cognatus* (Walker), MEXICO: TABAS-CO: Villa Hermosa, 16 July 1963, A. R. Gillogly (LACM), dorsal (1) and ventral (2) views. **3–4,** *M. clenchi*, holotype, dorsal (3) and ventral (4) views. **5–6,** *M. mathani* (Schaus), PERU: Tingo Maria, 9–10 Feb. 1977, J. R. Robertson (LACM), dorsal (5) and ventral (6) views. (All to same scale.)

African *Noctua crassa* Drury (1782: Pl. 2, Fig. 1), which was desig-nated by several subsequent authors and which has been erroneously accepted as the type species by virtually every worker in this century.

In addition to the geographical distribution and color pattern, *Mor-pheis* differs strikingly from *Xyleutes* Hübner (1820: 194) in the male genitalia; although the two are similar in basic structure, *Morpheis* has a massively developed gnathos (absent in *Xyleutes*) and lacks the sclerotized digitate process on the aedeagus of *Xyleutes*. Additionally, in the species of *Morpheis* examined to date, there is a digitate pro-cess on the sacculus (absent in *Xyleutes*), although it may sometimes be minute (*cognatus*).

Morpheis clenchi Donahue, new species
Fig. 3, 4, 7–9

Diagnosis. The strongly contrasting black (or dark brown) and white wing pattern, with reduced striations, black disc of thorax, and dark gray to blackish dorsum of abdomen readily distinguish this species. It is the largest zeuzerine known from the United States or adjacent northern Mexico.

Male.   Head: Antennal shaft dark brown with scattered white scales, bipectinate to about one-half (24–29 segments), rami light brown, then uniserrate and dark brown to tip. **Labial palpi** cylindrical, smoothly scaled, brownish-black, first segment paler. Vestiture of **frons** fine, hair-like, semi-erect, dark brown to blackish scales with bluish reflection in certain light; scales more erect on center of frons above end of palpi, forming a bilobed tuft. **Vertex** with prominent tuft of brown, hair-like scales ventrad of base of antennae; inter-antennal area with a long shaggy "crest" of loose, brownish-black hair-like scales. **Thorax:** Vestiture of pronotum concolorous with and in continuation of inter-antennal "crest"; disc of thorax concolorous brownish-black, the scales becoming gradually more spatulate and more appressed posteriorly, with a whitish spot on posterolateral corners of metathorax. **Tegula** bright white, scales long, slender, appressed. **Venter** dark grayish brown, scales hair-like and loose. **Legs** blackish-brown, distal ends of all tibiae and tarsal segments, and tibial spurs, whitish. **Abdomen:** Vestiture of fine, hair-like, appressed scales, dorsally gray to fuscous, paler on anterior edge of each segment (forming ill-defined, narrow, transverse bands); lateral pale line present, diffuse, anteriorly white (in continuation of white posterolateral thoracic spot), posteriorly becoming grayer; venter grayish to pale brown, not or poorly differentiated from lateral coloration; genital scaling fine, hair-like, mixed gray and brownish.

Wings.   Ground color chalky white, markings of forewing upperside brownish-black, of hindwing dark gray except for brownish-black spots on outer margin at vein ends. **Wing scales** short, spatulate, appressed, except: long, slender, with notched apex, and erect in base of forewing discal cell upperside; short, spatulate, erect in discal and accessory cells, and posteriorly to vein 2A on forewing upperside; long, hair-like on hindwing upperside in basal portion of area between discal cell and inner margin; forewing underside with mixed long hair-like and long spatulate scales in discal and accessory cells and posteriorly to vein 1A and in bases of cells between veins M_2 and Cu_2. **Forewing upperside** (Fig. 3): dominant color pattern an irregular longitudinal brownish-black stripe extending distally from basal 30% of costa through discal cell to and filling basal ¾ of cell M_2-M_3, then narrowing and continuing to outer margin in cell R_4-R_5; the anterior edge of stripe bounded by vein M_2, with several small, dentate projections anteriorly in cell M_1-M_2; posterior margin of stripe bounded by posterior side of discal cell with several small dentate or linear projections below discal cell, then expanding to form a large, quadrate projection from before origin of vein Cu_2 to vein 1A, the posterior margin of stripe then continuing distally and irregularly across bases of cells Cu_2-1A, Cu_1-Cu_2, and M_3-Cu_1, the last cell with one or more posterior projections partially or completely enclosing the ground color to form one or more open or closed white circles, then across cell M_2-M_3, narrowing abruptly at vein M_2 and then to outer margin at end of vein R_5. This longitudinal stripe very sparsely irrorate with minute white scales (invisible to the naked eye in greasy specimens). Remaining brownish-black markings consisting of a series of small costal spots, the largest a blotch at ⅔, at end of vein Sc, followed by smaller blotches at ends of veins R_1, R_2, and R_3; a series of small subcostal spots, usually complete to end of vein R_3; a series of small spots in accessory cell; a series of small, irregular spots in cell R_3-R_4; a series of transverse marks in cell R_5-M_1, the outermost fusing with the main longitudinal stripe; subterminal white space between veins M_1 and Cu_2 sparsely irrorate, occasionally appearing striate; a series of short striations in cell 1A-2A, fusing with the quadrate projection below origin of vein Cu_2; very variable irroration of the remaining white ground color, usually most prominent as well-spaced short striations on inner margin and in cell Cu_2-1A. Fringe white except at distal end of longitudinal stripe in vicinity of end of vein R_5, and terminal spots on veins R_4 to 2A. All veins concolorous

with ground color and color pattern. **Hindwing upperside** white with an irregular, prominent, broad, fuscous, striate, sub-reticulate shade through center of wing from vein 2A across lower corner of cell to outer margin at end of vein M_1, and only partially filling cell R_5-M_1; the shade usually radiating distally along posterior margins of veins, and becoming distally striate in cells between veins Cu_2 and 2A. Costa white, tending to be striate distally, with a longitudinal fuscous patch along distal end of vein Sc+R_1. Fringe white, with brownish black terminal spots on ends of veins R_s to 2A. **Underside** (Fig. 4) color pattern of both wings similar to that of upperside, ground color duskier, with the following exeptions: **Forewing underside:** basal costal patch absent, indicated only by dark leading edge of costa; longitudinal stripe originating in center of cell, formed by long gray scales in cell, and distad of cell by dark brown scales with intermixed paler scales (bluish in certain light), producing the effect of a more diffused, less well-defined pattern than on upperside; striations less sharply defined; **Hindwing underside** with additional diffuse brownish discal patch present, extending obliquely (in well-marked specimens) from anterior half of cell nearly to costa, most evident as an irregular, offset patch on vein Sc at ½; costa striate from this patch to near apex.

Genitalia (Figs. 7–9). As illustrated, proximal half of digitate process of sacculus fused to valva, the distal half free. A thorough survey of the genus is required before the significance of any differences in genitalic structure among the species can be appreciated.

Size (measured to nearest mm). Forewing length 28–36 mm, mean 33 ± 2.34 mm (n = 13).

Female. Unknown, probably similar to male in appearance but larger, with antennae uniformly filiform or minutely uniserrate.

Early Stages. Unknown; larva undoubtedly a borer in roots or wood, as in other members of the family.

Types: Holotype ♂, ARIZONA: Santa Cruz Co., 5 mi. W of Peña Blanca, 28 July 1973, at ultraviolet black light, R. Wielgus (LACM). Paratypes: 12 ♂, distributed as indicated, all from ARIZONA: Santa Cruz Co. Peña Blanca Lake, Oro Blanco Mountains, 10 air mi. WNW of Nogales, elev. 3700 ft.: 2 ♂, 19 July 1976, E. M. Brown & J. S. McElfresh (Brown & McElfresh); 2 ♂, 24 July 1973, W. A. Harding (LACM); 1 ♂, 28 July 1973, Bruce Griffin (Frack); 2 ♂, 26 July 1973, R. J. Ford (1, LACM; 1, Arizona State University). Peña Blanca: 2 ♂, 7 July 1972, at black light, D. C. Frack (1, LACM; 1, Frack). Peña Blanca Lake: 1 ♂, 12 July 1967, K. Roever (Lloyd M. Martin). Campground, near Peña Blanca Lake, elev. 3950 ft.: 1 ♂, 27 July 1976, at ultraviolet light, J. Wiseman (LACM). Sycamore Canyon: 1 ♂, 16 July 1974, D. G. Marqua (Marqua).

Etymology. I take great pleasure in naming this moth in honor of the late Harry K. Clench, who had a research interest in the Cossidae before he succumbed to the lure of fulltime work on butterflies. He generously gave me a copy of his unpublished draft revision of the New World Zeuzerinae, with his blessing to continue work where he left off. This paper is the first of a series of papers on the Cossidae, a project stimulated in large part by Harry's encouragement and cooperation.

Remarks. As noted above, this moth has only been collected during July, in the Peña Blanca and Sycamore Canyon area of southern Arizona. It undoubtedly occurs in adjacent Mexico, and is perhaps more widespread in Arizona.

The three known species of the *cognatus* group of *Morpheis* are distinguished from other members of the genus by the white ground color of the forewing, with strongly contrasting dark color patches, and by the greatly reduced transverse striations.

Key to species of the *cognatus* group of *Morpheis* (males)

1a. Disc of thorax black, contrasting sharply with white tegulae; dorsum of abdomen dark gray to fuscous, weakly annulated with paler scales (Arizona) _____ *clenchi* Donahue, n. sp.
1b. Disc of thorax and tegulae concolorous, white; disc with sharply defined, narrow, longitudinal brown or black line; dorsum of abdomen white, with or without a median line _____ 2
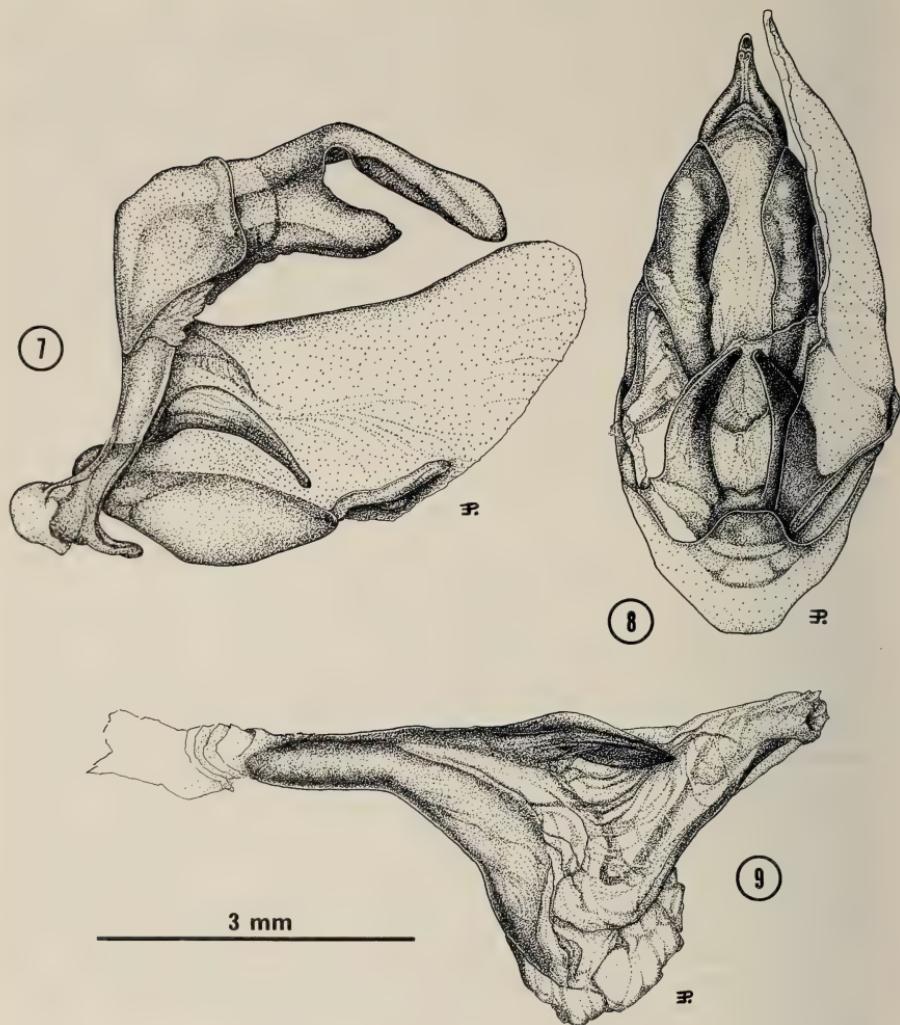
FIGS. 7–9. Male genitalia of *Morpheis clenchi*, paratypes. **7,** left lateral view, aedeagus and left valva removed, ARIZONA: Santa Cruz Co., Peña Blanca Lake, Oro Blanco Mts., 10 air mi. WNW Nogales, elev. 3700 ft., 26 July 1973, R. J. Ford (LACM). **8,** ventral view of same specimen, aedeagus and left valva removed. **9,** left lateral view of aedeagus (vesica not fully everted), figured from a second specimen, same locality, 24 July 1973, W. A. Harding (LACM). (All to same scale.)

2a. Larger species (forewing length 40–50 mm); abdomen with distinct mid-dorsal black line on distal half (Peru) ------------------------------------ *mathani* (Schaus)
2b. Smaller species (forewing length 18–30 mm); mid-dorsal dark line of abdomen indistinct or absent (Mexico to Honduras; southern limit of distribution not established) -- *cognatus* (Walker)

Although this paper is not a generic revision, it seems appropriate to associate all those species which appear to belong to *Morpheis*. The synonymy is based largely on previously published work, but a few taxa are reclassified here as proposed by Clench (in his manuscript revision of the New World Zeuzerinae). Since I have not examined all these species and their types, this classification is tentative.

Proposed classification and synonymy of *Morpheis*

Morpheis Hübner [1820: 196]; Type-species: *Sphinx pyracmon* Cramer, 1780: 169, designated by Roepke, 1957: 18. (Gender: Masculine.)
    = *Neocossus* Houlbert, 1916: 89; Type species: [*Endoxyla*] *strigillata* C. Felder, 1874: Pl. 81, Fig. 5, by original designation. New Synonymy.
    = *Xylotrypa* Turner, 1918: 162; Type species: [*Endoxyla*] *strigillata* C. Felder, 1868: Pl. 81, Fig. 5, by original designation and monotypy. New Synonymy.
    = *Xyleutes* of authors, in part, not Hübner [1820: 195].
xylotribus (Herrich-Schäffer, [1853] 1850–1858: Figs. 37, 38) (*Cossus*), New Combination.
pyracmon (Cramer, 1780: 169) (*Sphinx*).
    = *putridus* (Percheron, 1838: Pl. 4, Fig. 1) (*Zeuzera*), New Combination.
    = *palmarum* (Herrich-Schäffer, [1853] 1850–1858: Fig. 36) (*Cossus*), New Combination.
    = *fractus* (Walker, 1856: 1542) (*Zeuzera*), New Combination.
    = *pyracmonides* (Schaus, 1901: 45) (*Duomitus*), New Combination.
discretus (Dyar & Schaus, 1937: 1267) (*Xyleutes*), New Combination.
comisteus (Schaus, 1911: 628) (*Zeuzera*), New Combination.
lelex (Dognin, 1891: 121) (*Zeuzera*), Revised status, New Combination.
strigillatus (C. Felder, 1874: Pl. 81, Fig. 5) (*Endoxyla*), New Combination.
impeditus (Wallengren, 1860: 44) (*Phragmataecia*) (see Gaede, 1933: 822), New Combination.
melanoleucus (Burmeister, 1878: 407) (*Cossus*), New Combination.
votani (Schaus, 1934: 95) (*Xyleutes*), New Combination.
cognatus (Walker, 1856: 1532) (*Zeuzera*), New Combination.
    = *mexicanus* (Houlbert, 1916: 88) (*Xyleutes*, subgenus *Neocossus*), New Combination.
mathani (Schaus, 1901: 45) (*Duomitus*) Revised status, New Combination.
    = *oberthueri* (Houlbert, 1916: 86) (*Xyleutes*, subgenus *Neocossus*), Emendation, Revised Synonymy, New Combination.
    = *cognatus*, in part, in the sense of Dyar & Schaus, 1937: 1267, not Walker, 1856: 1532.
    = *cognatus distinctus* (Bryk, 1953: 267) (*Xyleutes*), New Synonym, New Combination.
clenchi Donahue, new species

Eugenia Scott Paul, who volunteered her talents to prepare the genitalic figures, and to Larry Reynolds, LACM staff photographer, for the photographs. I am indebted to Allan Watson of the British Museum (Natural History) for bibliographic assistance and the loan of comparative material, and to Charles L. Hogue for his helpful critique of the manuscript. I am particularly grateful to George C. Steyskal for his nomenclatorial assistance, which resulted in the many changes in spelling of the included species and their synonyms.

Literature Cited

Bryk, F. 1953. Lepidopteren aus dem Amazonasgebiete und aus Peru gesammelt von Dr. Douglas Melin und Dr. Abraham Roman. Ark. Zool., Stockholm (n.s.) 5: 1–268.

Burmeister, H. C. C. 1878. Description physique de la République Argentine d'après des observations personelles et étrangères. Vol. 5, *Lépidoptères*. Pt. 1, Diurnes, Crépusculaires et Bombycoides. vi + 524 p. Buenos Aires.

Cramer, P. 1780. De Uitlandsche Kapellen Voorkomende in drie Waereld-deelen Asia, Africa en America. Vol. 3. 176 p., pls. 193–288. Amsterdam.

Dalla Torre, K. W. von. 1923. Lepidopterorum Catalogus. Pars 29: Cossidae. 63 p. Berlin.

Dognin, P. 1891. Diagnoses de quelques Héterocères du Vénézuéla. Le Nat. 13: 121.

Drury, D. 1782. Illustrations of Natural History, ... vol. 3. 15 + 76 p., 50 col. pls. London.

Dyar, H. G. & W. Schaus. 1937. Cossidae. pp. 1264–1287 *in* Seitz, A., The Macrolepidoptera of the World. Vol. 6, The American Bombyces and Sphinges. 1328 p. (English edition, incomplete). Stuttgart.

Fabricius, J. C. 1775. Systema Entomologiae sistens Insectorum classes, ordines, genera, species, adjectis synonymis, locis, descriptionibus, observationibus. 832 p. Flensburgi & Lipsiae.

Felder, C. *in* Felder, C. & Alois F. Rogenhofer. 1874. Reise der österreichischen Fregatte Novara um die Erde, in den Jahren 1857, 1858, 1859, unter den Befehlen des Commodore B. von Wüllerstorf-Urbair. Zoologischer Theil. Bd. 2, Abtheil. 2: Lepidoptera. Heft 4. 9 p., 120 col. pls. Wien.

Forbes, W. T. M. 1942. The Lepidoptera of Barro Colorado Island, Panama. No. 2. Bull. Mus. Comp. Zool., Harvard 90: 263–406.

Gaede, M. 1933. Cossidae. pp. 807–824. *In* Seitz, A., Die Gross-Schmetterlinge der Erde. Bd. 10. Die Indo-Australischen Spinner und Schwarmer. 909 p., 104 col. pls. Stuttgart.

Grote, A. R. H. [1866] 1865. Notes on the Bombycidae of Cuba. Proc. Entomol. Soc. Phila. 5: 227–255.

Hampson, G. F. 1892. The Fauna of British India, including Ceylon and Burma. Moths. Vol. I. xxiii + 527 p., 333 figs. London.

Herrich-Schäffer, G. A. W. [1853–1858]. 1850–1858. Sammlung neuer oder wenig bekannter aussereuropäischer Schmetterlinge. Vol. 1, Ser. 1. Heterocera. 551 figs. Regensburg.

Houlbert, C. 1916. Sur la distribution géographique des *Xyleutes* (Lép. Zeuzeridae) et description de sept espèces nouvelles. *In* Études de Lépidoptérologie Comparée (Charles Oberthür). Fascicule XI bis, pp. 63–120, 36 figs. Rennes.

Hübner, J. 1816–1826. Verzeichniss bekannter Schmettlinge [sic!]. 431 p. Augsburg.

Kirby, W. F. 1897. A Hand-Book to the Order Lepidoptera. Lloyd's Natural History. vol. 5, Moths, Pt. 3. xii + 332 p., 52 figs., 31 col. pls. London.

Lima, A. da Costa. 1945. Insetos do Brasil. Vol. 5. Lepidopteros, Parte 1. 379 p., 235 figs. Escola Nacional de Agronomia [Brasil], Série Didática No. 7.

LINNAEUS, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. 10th ed. Vol. 1. 824 p. Laurentii Salvii, Holmiae.

PERCHERON, A. R. 1835–1838. Genera des Insectes ou exposition détaillée de tous les caractères propres à chacun des genres de cette classe d'animaux. Livr. 6. Lépidoptères. (unnumbered pages). Paris.

ROEPKE, W. 1957. The cossids of the Malay region (Lepidoptera: Heterocera). Verhandl. Koninkl. Ned. Akad. Wetensch. afd. Nat. Tweede Reeks 52(1): 1–60.

SCHAUS, W. 1901. New species of Heterocera from tropical America. I. J. New York Entomol. Soc. 9: 40–48.

———— 1911. New species of Heterocera from Costa Rica. VIII. Ann. Mag. Nat. Hist. (8) 7: 612–634.

———— 1934. New species of Heterocera from tropical America. Ann. Mag. Nat. Hist. (10) 14: 79–115.

TURNER, A. J. 1918. Observations on the lepidopterous family Cossidae and on the classification of the Lepidoptera. Trans. Entomol. Soc. Lond. 1918: 155–190.

VIETTE, P. E. L. 1951–1952. Contribution à l'étude des Cossidae (2e note). Les genres et leur espèce type. Lambillionea 51: 37–43, 58–60, 68–72.

WALKER, F. 1856. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum. Part VII. Lepidoptera Heterocera. pp. 1509–1808. London.

WALLENGREN, H. D. J. 1860. Lepidopterologische Mittheilungen. Wien. Ent. Monatschr. 4: 33–46, 161–176.

TWO NEW SPECIES OF *PROEULIA* FROM THE DESVENTURADAS ISLANDS (TORTRICIDAE)

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ABSTRACT.   The species *Proeulia clenchi* and *P. kuscheli* are described.

In November 1960, Dr. Guillermo Kuschel visited San Ambrosio in the Desventuradas Islands (Chile), and made a small collection of Lepidoptera, mostly Microlepidoptera. As far as I can ascertain, no Lepidoptera have been recorded previously from this island group.

The genus *Proeulia* apparently is restricted to mainland Chile and nearby islands. Clarke (1962, 1965) recorded two species from the Juan Fernandez Islands and Obraztsov (1964) recorded nine species from central Chile. The two species described in this paper bring the total for the genus to thirteen and extend the range to the Desventuradas.

Genus *Proeulia* Clarke

Proeulia Clarke, 1962, p. 293. (Type species: *Eulia robinsoni* Aurivillius, 1922, *in* Skottsberg, The Natural History of Juan Fernandez and Eastern Island, 3(part 2): p. 266, Pl. 11, Fig. 17 [by original designation].)

Proeulia clenchi Clarke, new species
Fig. 1, 3, 5

Description.   Wing expanse 20–22 mm. Labial palpus pale ochraceous buff; second segment suffused grayish on outer side; third segment suffused grayish. Antenna grayish fuscous. Head buff, speckled grayish fuscous anteriorly. Thorax buff, suffused grayish fuscous, tegula buff. Forewing ground color pale ochraceous buff with scattered grayish fuscous irroration; along costa a series of small grayish-fuscous dots; from middle of costa an ill-defined outwardly oblique grayish-fuscous fascia extends to base of veins 2 and 3; in some specimens, along dorsum, ill-defined grayish-fuscous spots; cilia grayish-fuscous. Hindwing pale buff mottled grayish fuscous. Foreleg buff; tibia and tarsal segments marked grayish fuscous; midleg and hindleg buff with little or no grayish suffusion. Abdomen grayish fuscous dorsally; buff ventrally.
   Male genitalia.   USNM 24766. Harpe about twice as long as broad, cucullus rounded; sacculus thickened distally ending in a point; costa not appreciably sclerotized. Gnathos curved, broad distad, terminating in a point. Uncus very slender, curved. Socius long, pendant. Vinculum U-shaped. Tegumen about as long as broad. Anellus a sclerotized plate with a median protuberance. Transtilla a simple lightly sclerotized band with a median posterior point. Aedeagus moderately stout, bluntly pointed; cornuti two, one long and flattened, the other slender and shorter (in the figure, one is superimposed over the other and the two appear as one).
   Female genitalia.   USNM 24767. Ostium very broad. Inception of ductus seminalis from ventral surface of bursa copulatrix near cestum. Ductus bursae very short, membranous. Bursa copulatrix pearshaped, inner surface lightly rugose; cestum a pointed protrusion.
   Type.   Holotype: USNM 76531. Described from the Holotype ♂, San Ambrosio

FIGS. 1–2. **1,** *Proeulia clenchi*, new species: Holotype ♂. **2,** *Proeulia kuscheli*, new species: Holotype ♂. Photograph by V. E. Krantz.

Island, elev. 450 m, 8 Nov. 1960 and 3 ♂ and 2 ♀ paratypes from the same locality, elev. 400–450 m, collected 8–14 Nov. 1960.

Remarks. *Proeulia clenchi* appears to be most closely related to *P. auraria* (Clarke) (1949, p. 583) but differs from it by the darker ground color of forewing, the broader cucullus and the shorter cestum. The known distribution is San Ambrosio Island.

FIGS. 3–4. **3,** *Proeulia clenchi,* new species: ventral view of male genitalia with aedeagus on right. **4,** *Proeulia kuscheli,* new species: ventral view of male genitalia with aedeagus on right. Photograph by V. E. Krantz.

This species is named in honor of the late Harry K. Clench who is greatly missed by all of us.

Proeulia kuscheli Clarke, new species

Figs. 2, 4

Description. Wing expanse 18 mm. Labial palpus olive; second segment white on most of inner side and ventrally. Antenna olive. Head olive with scattered whitish
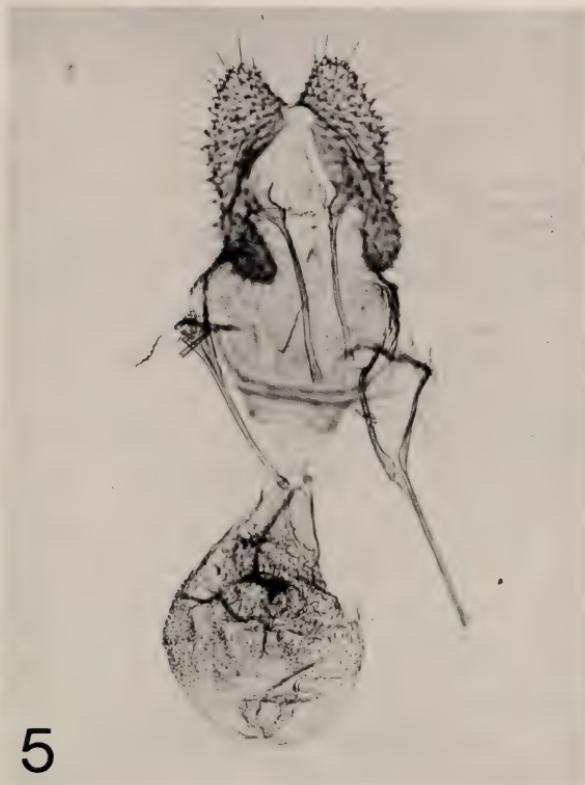
FIG. 5.   *Proeulia clenchi*, new species: ventral view of female genitalia. Photograph by V. E. Krantz.

scales. Thorax olive with a few whitish scales posteriorly; tegula white-tipped. Forewing ground color olive, without discernible contrasting markings; cilia concolorous. Hindwing white except for olive coloring around margins. Foreleg white overlaid olive on outer side; midleg similar; hindleg whitish; tarsal segments marked olive. Abdomen olive dorsally, ventrally grayish with olive irroration.

Male genitalia.   USNM 24765. Harpe broadest at base, gently tapered to the rounded cucullus; sacculus fleshy, produced as a blunt point distally; costa strongly sclerotized. Gnathos rather broad, curved, and triangular distally. Uncus very slender, curved. Socius long, pendant. Vinculum narrowly U-shaped. Tegumen subtriangular, very strongly sclerotized laterally. Anellus a sclerotized plate with a median bulge. Transtilla a simple, lightly sclerotized band, narrowest at middle. Aedeagus stout, strongly angled subbasally, distally pointed; cornuti two, very long, one slightly longer than the other.

Type.   Holotype: USNM 76530. Described from the Holotype ♂, San Ambrosio Island, elev. 450 m. The holotype is labeled "on flowers of *Thamnoseris lacerata* Phil."

Remarks.   This species is distinguished from any other described member of the genus by the solid ground color of the forewing and its olive-bordered white hindwing.

It gives me great pleasure to name this species in honor of my good friend Dr. Guillermo Kuschel, collector of the specimen.

LITERATURE CITED

CLARKE, J. F. GATES. 1949. Notes on South American "Tortricidae" (Lepidoptera) and descriptions of new species. De Acta Zoologica Lilloana del Instituto "Miguel Lillo" 7: 579–588.

———— 1962. A new tortricid genus from South America. Proc. Biol. Soc. Washington 75: 293–294.

———— 1965. Microlepidoptera of Juan Fernandez Islands. Proc. U.S. National Museum 117(3508): 1–105.

OBRAZTSOV, N. S. 1964. Neotropical Microlepidoptera. V. Synopsis of the species of the genus *Proeulia* from central Chile (Lepidoptera: Tortricidae). Proc. U.S. National Museum 116(3501): 183–195.

A REDESCRIPTION OF "*MICROPTERYX*" *SELECTELLA* WALKER WITH A DISCUSSION CONCERNING ITS FAMILY AFFINITIES (ACROLEPIIDAE)

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ABSTRACT. The Holotype of "*Micropteryx*" [sic] *selectella* Walker is re-examined and illustrated. On the basis of head structure, wing venation, abdominal articulation, and male genitalia, it is concluded that the species demonstrates closest relationship to the genus *Antispastis* of the Acrolepiidae.

In the course of investigations on primitive Lepidoptera, particularly the Micropterigidae and Incurvariidae, I found it necessary to examine a curious little species collected by William Bates in the Amazon during his residency there from 1848 until 1859. This virtually unknown species, represented by a unique male, was described by Walker (1863) in the genus *Micropterix*. Meyrick (1912) later transferred the species to the genus *Adela*. Because neither of these two genera are believed to exist in the Amazon basin, it is significant, both from the standpoint of biogeography as well as of systematics, to determine the proper family affinities of this insect.

In contrast to both Walker's and Meyrick's superficial conclusions, "*Micropterix*" *selectella* is without question a member of a ditrysian family. In both venation and male genital structure, it appears most similar to *Antispastis xylophragma* Meyrick, as figured by Clarke (1969). The latter differs somewhat from *selectella*, particularly by the stalked condition of M_1 and M_2 of the hindwing. Consequently, it is possible that although the two species may be closely related, they may not be congeneric. Until further study, however, it seems advisable to place *selectella* in *Antispastis* Meyrick. The venation of *Machlotica chrysodeta* Meyrick appears more similar to *selectella*, but the male genitalia of these two species differ strikingly.

Some uncertainty also persists concerning the family placement of *Antispastis*. Meyrick (1926) originally placed the genus in Glyphipterigidae, and that decision has been followed to the present. Heppner (personal communication), after reviewing most of the glyphipterigid genera, now believes that *Antispastis* is more related to *Acrolepia*, a member of the yponomeutoid family Acrolepiidae. I concur with this opinion, particularly on the basis of the observed similarities of the male genitalia of *Antispastis* and *Acrolepia*.

The abdominal articulation of *Antispastis selectella* is similar to that of Acrolepiidae and other families of the primitive ditrysian stock in possessing the "tineoid" type of apodemes as discussed by Brock

Fig. 1. *Antispastis selectella*; ♂ holotype. Wing expanse 7.8 mm; Tefé, Brazil.

(1968). The apodemes in *A. selectella* consist of a pair of elongate, slender and slightly curved rods which project free far beyond the cephalic margin of the second abdominal sternite. The free portion of the apodemes contunues internally as a tapering, sclerotized bar posteriorly along the sternite.

A more complete description of *Antispastis selectella* (Walker) may be summarized as follows:

Antispastis selectella (Walker), new combination

Figs. 1–5

Micropteryx [sic] *selectella* Walker, 1863: 495.
Adela selectella (Walker). Meyrick, 1912: 11.

Adult (Fig. 1). Wing expanse: ♂, 7.8 mm; length of forewing 3.5 mm.
Head. Vestiture smooth (but badly rubbed in unique holotype), consisting of moderately broad, stramineous scales interspersed with more narrow, hairlike scales of same general color. Antennae broken near base but with basal 3 to 5 segments intact, stramineous, ringed with fuscous apically on each segment; scales appressed, with venter of flagellum mostly naked, except for short, pale pubescence; scape without pecten. Ocelli present. Labrum and pilifers extremely reduced, with a short tuft of stramineous setae arising from each pilifer. Maxillae with haustellum essentially naked except for very short, pale pubescence; haustellum coiled in repose, exceeding length of labial palpi; maxillary palpi minute, apparently consisting of one short segment. Labial palpi 3-segmented, mostly porrect though slightly upturned; third segment elon-
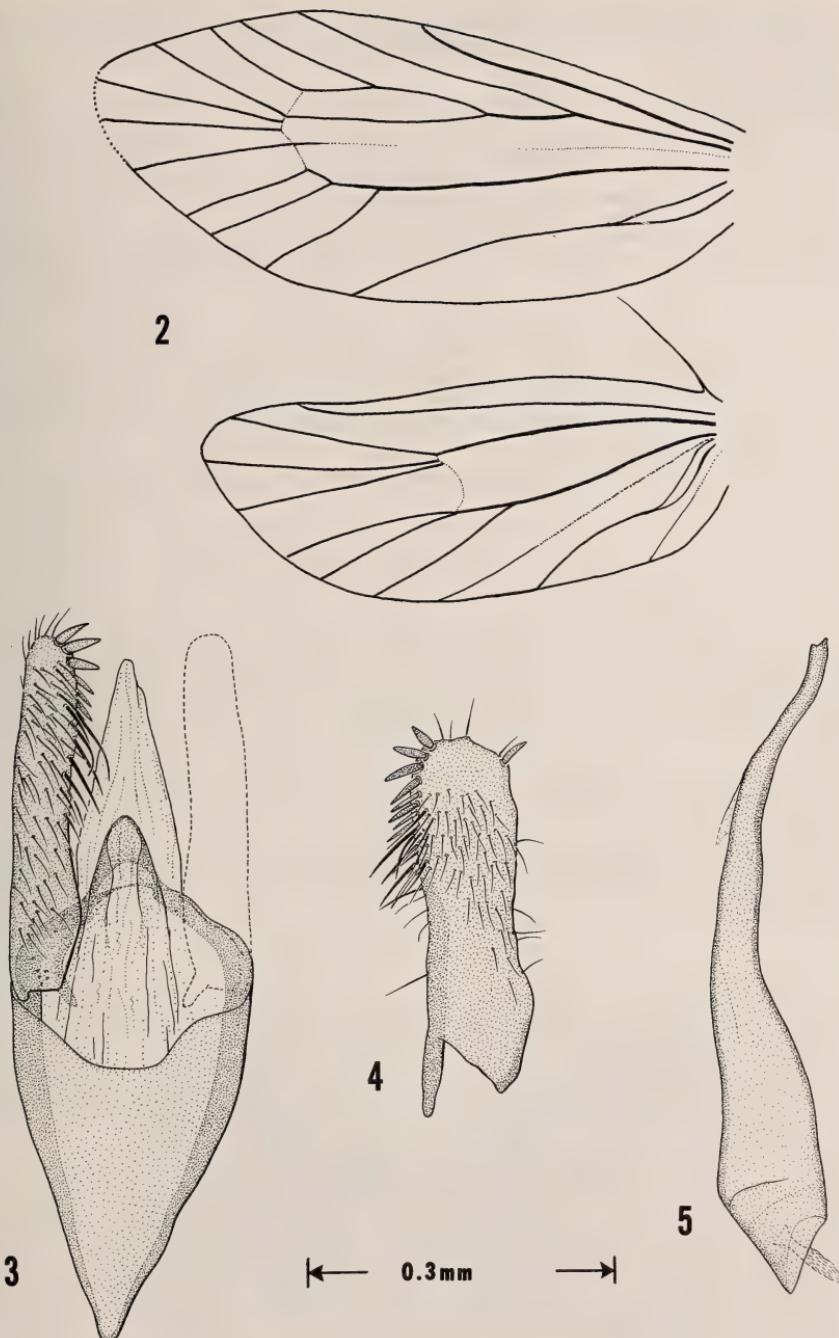
FIGS. 2–5. *Antispastis selectella*. **2**, Wing venation. **3**, ♂ genitalia, ventral view. **4**, Valva of genitalia, lateral view. **5**, Aedeagus, lateral view (scale = 0.3 mm).

gate, slightly exceeding length of second; apex acute; vestiture relatively smooth, without ventral tufts, stramineous with a suffusion of brownish fuscous ventrally, especially on third segment.

Thorax. Dorsum (badly rubbed) covered with broad, brownish fuscous scales with a slight golden-bronze luster. Venter whitish to stramineous with a silvery sheen. Prothoracic and mesothoracic femora largely stramineous, not banded; tibiae darker, brownish fuscous, with a broad stramineous band encircling base; prothoracic tibiae with a prominent epiphysis; mesothoracic tibiae with a single pair of well developed spurs, one member of pair nearly 2.0× the length of other; each spur stramineous dorsally and fuscous ventrally; tarsal segments of pro- and mesothoracic legs fuscous, banded with whitish to stramineous; mesothoracic tarsi with three broad bands dorsally which tend to coalesce distally underneath. Forewings mostly brownish fuscous with a strong golden-bronze iridescence; basal third of wing with single broad yellowish fascia with parallel sides; width of fascia approximately equal to width of head; a somewhat indistinct, incomplete blackish fascia extending from midway along costa about halfway across wing; width of black fascia slightly less than that of yellow fascia; fringe uniformly brownish fuscous. Hindwings distinctly paler in color, uniformly covered with broad grayish scales.

Abdomen. Uniformly brownish fuscous dorsally and ventrally. Eighth segment with moderately long hair pencils.

Male genitalia (Figs. 3–5) Uncus absent. Tegumen reduced to a narrow ring dorsally. Vinculum well developed, triangular, nearly equalling length of valvae. Valvae relatively simple, approximately same width throughout with sacculus only slightly evident; apex terminating in a rather symmetrically rounded cucullus; costal apex of valva with 6 to 8 large peglike setae arranged in a single marginal series; a single peglike seta present at lower angle of cucullar margin. Annellus slightly sclerotized dorsally and produced into a partially membranous conical process extending noticeably beyond caudal apex of tegumen. Aedeagus elongate, approximately 1.7× the length of valvae and relatively simple, slightly sinuate, without cornuti or exterior processes.

Type. Holotype, ♂; in the British Museum (Natural History). **Type locality.** Ega [=Tefé], Brazil.

Host. Unknown.

Distribution. Known only from the type locality of Tefé (formerly Ega) which is located on the Rio Tefé near its junction with the Amazon River in the state of Amazonas, Brazil.

LITERATURE CITED

BROCK, J. P. 1968. The systematic position of the Choreutinae (Lep., Glyphipterygidae). Entomol. Monthly Mag. 103: 245–246.

CLARKE, J. F. G. 1969. Catalogue of the type specimens in the British Museum (Natural History) described by Edward Meyrick, vol. 6, Glyphipterigidae, Gelechiidae (A–C), London. 537 p.

MEYRICK, E. 1912. Adelidae, Micropterygidae [sic], Gracilariadae [sic]. Pages 1–68 *in* H. Wagner (editor), Lepidopterorum Catalogus, Par. 6.

WALKER, F. 1863. List of the specimens of lepidopterous insects in the collection of the British Museum, vol. 28, Tortricites and Tineites. London, 561 p.

A NEW SPECIES OF *XENIMPIA* FROM MADAGASCAR (GEOMETRIDAE)

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ABSTRACT. The new species *Xenimpia clenchi* is described from Madagascar. It is compared with the two other known endemic species in the genus, *X. trizonata* and *X. fletcheri*.

Two species of the genus *Xenimpia* W. Warren (1895) are known from Madagascar: *X. trizonata* (Saalmüller) 1891 (=*trivittata* P. Mabille 1900) and *X. fletcheri* Herbulot, 1954 (Herbulot 1957: 247). A third species is described here. This new species is dedicated to the memory of my friend and colleague, Harry K. Clench of the Carnegie Museum.

Xenimpia clenchi Viette, new species

Figs. 1–4

Forewing length (base to apex) Holotype ♂, 17 mm; Paratype ♀, 18 mm.

Male. Antennae long bipectinated, buff. Labial palpi brown grey, with the third segment darker. Head, patagia, tegulae and thorax light grey. Abdomen dark grey speckled with brown. Legs grey with the external site of the fore tibiae brown; tibiae and segments of the tarsi thin and lengthened.

Fore- and hind-wings uniformly dark grey slightly irrorated with brown. A yellowish brown patch at the end of the discoidal cell. Cilia concolorous with the ground. Outer margin of the hindwings with a very short tail at vein M_1. Underside almost identical to upperside, but the ground color is paler.

Male genitalia. Eighth abdominal tergite with two caudal and lateral points. Uncus triangular to the base, typical in its distal part. Vinculum with a short saccus. Valvae showing externally a dorsal arm and a ventral lengthened lobe; apex of the arm with
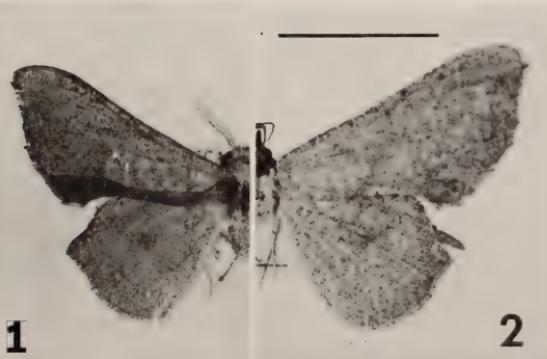
FIGS. 1–2. *Xenimpia clenchi*, new species. **1,** Holotype ♂; **2,** Paratype ♀. Scale line = 1 cm. Photograph by M. Franey.
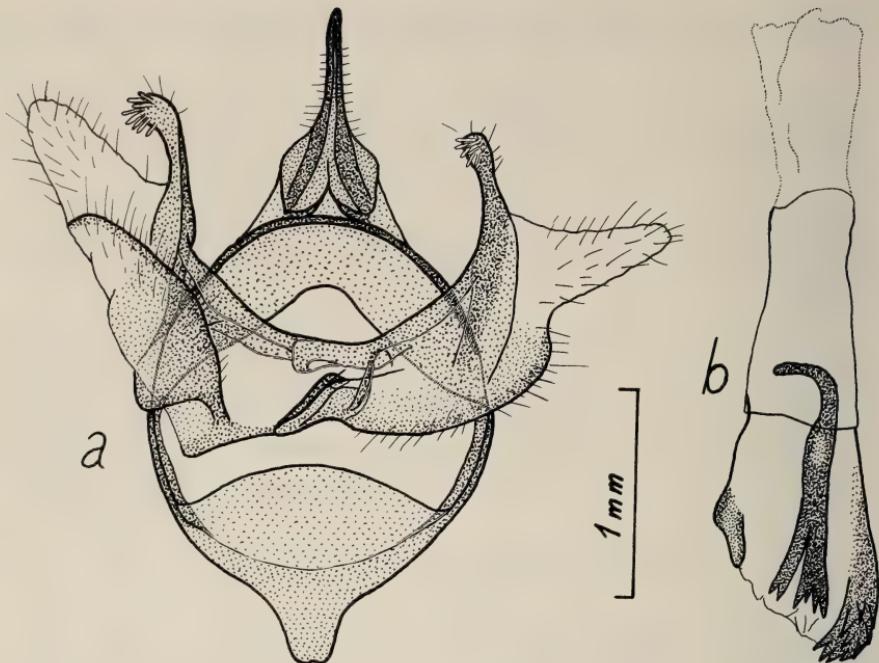
FIG. 3. a, ♂ genitalia and b, aedeagus of Holotype specimen of *Xenimpia clenchi*, new species. Drawing by J. Boudinot.
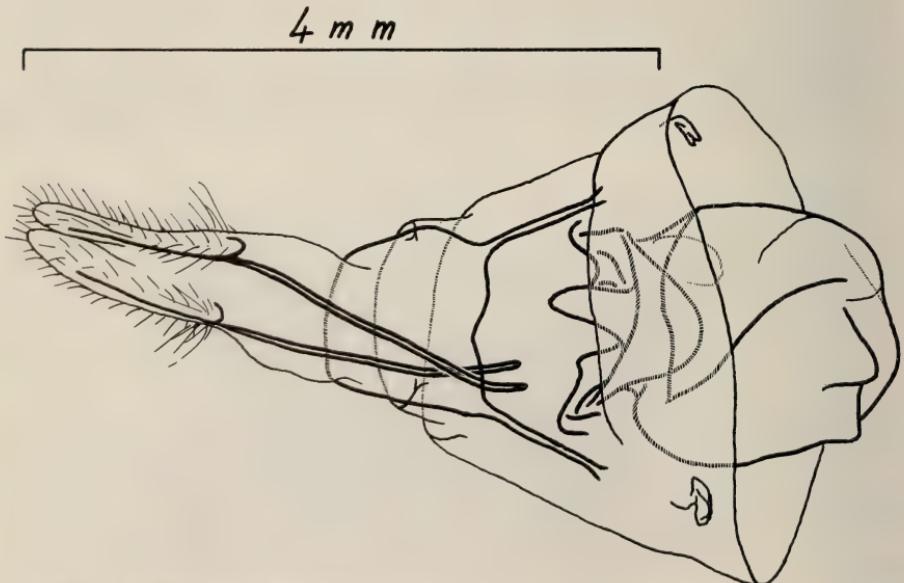
FIG. 4. ♀ genitalia of Paratype specimen of *Xenimpia clenchi*, new species. Drawing by J. Boudinot.

short spines. Aedeagus stout, enlarged and flattened in its distal half, heavily chitinized on the sides and membraneous in part. A strong cornutus proximally bent and distally bifid; every part is toothed at the apex.

Female.   Antennae serrate. Similar to male, but the ground color of the forewings is paler and, in the forewings, the postmedial band is indicated by some yellowish brown spots. Underside paler than upperside, with the outer yellowish spots more distinct and pointed out on the hindwings.

Female genitalia.   Papillae anales slightly sclerotized, narrow and lengthened. Posterior apophyses twice as long as the anterior apophyses. Eight abdominal tergite sclerotized, funnel shaped, with a small tongue in the middle. Ductus bursae very short. Corpus bursae slightly sclerotized, spheroid.

Holotype ♂.   Madagascar Centre, massif de l'Itremo, Haute Ikoly, ⅘ km NW of col de l'Itremo, 1600 m, 16/20 Feb. 1974 (P. Viette & A. Peyrieras) (genitalia slide, P. Viette no. 5638).

Paratype ♀.   Madagascar Centre, Ambatofinandrahana, 1180 m, 27 Aug. 1957 (P. Griveaud) (genitalia slide, P. Viette no. 5639).

Both in collection of Museum National d'Histoire Naturelle (Entomologie), Paris.

Remarks.   *X. clenchi* is, based on its wing pattern, close to *X. misogyna* Carcasson (1962: 60), from Kenya. It differs by the uniform ground color, which in *X. misogyna* is olive buff with a paler area in the middle of the hindwings.

Based on the male genitalia, *X. clenchi* is allied to *X. fletcheri* Herbulot (1954: 120), from Madagascar, but the appearance of these two species is entirely different. *X. fletcheri* is a sexually dimorphic species.

Literature Cited

Carcasson, R. H. 1962. New African Lepidoptera. J. E. Afr. Nat. Hist. Soc., 24(1): 54–68.

Herbulot, C. 1954. Nouveaux Geometridae malgaches. Mém. Inst. Sci. Madag., (E) 5: 81–123.

———— 1957. Liste des Ennominae de Madagascar (Lepidoptera Geometridae). Le Natural. Malg., 8(2) [1956]: 243–260.

Mabille, P. 1900. Lepidoptera nova malagassica et africana. Ann. Soc. ent. France, 68 [1899]: 723–753.

Saalmüller, M. 1891. Lepidopteren von Madagascar, Zweite Abth. [completed by L. von Heyden] pp. 249–531, pl. 7–14, figs. 99–279. Moritz Diesterweg, Frankfurt am Main.

Warren, W. 1895. New species and genera of Geometridae in the Tring Museum. Nov. Zool. 2: 82–159.

THE LYCAENID "FALSE HEAD" HYPOTHESIS: HISTORICAL REVIEW AND QUANTITATIVE ANALYSIS

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ABSTRACT. The wing pattern and behavior of lycaenid butterflies putatively create the impression of a head at the posterior end of the insect, and deflect predator attacks from the real head. I review components of wing pattern and behavior which contribute to the appearance of a head, quantify two of these behaviors in the Neotropical "false head" lycaenid, *Arawacus aetolus*, and suggest that one behavior—landing head downwards—does not enhance the deceptiveness of a "false head". I then examine two kinds of evidence—predator inflicted wing damage and observations of predator attacks—which test the "false head" hypothesis.

The study of protective coloration in insects (e.g. mimicry, industrial melanism) has been instrumental in the development and testing of evolutionary theory. A fascinating proposed example of protective coloration is the hypothesis that the wing pattern and behavior of lycaenid butterflies (Lycaenidae) create the impression of a head at the posterior end of the insect, thus deceiving predators into attacking the less vulnerable end of the butterfly. This "false head" hypothesis is discussed in books on protective coloration of animals (e.g. Cott, 1940; Wickler, 1968; Edmunds, 1974a) and general works on butterflies (e.g. Klots, 1951; D'Abrera, 1971; Owen 1971), but has not been comprehensively reviewed. As a result, authors of popular books omit important information concerning the "false head" hypothesis, particularly observations of predators attacking lycaenids. Furthermore, behaviors which putatively enhance the deceptiveness of these insects were described qualitatively, and to varying degrees, inaccurately. The purposes of this paper are to review the development of the "false head" hypothesis, and to supplement this account with quantitative data on the Neotropical "false head" lycaenid, *Arawacus aetolus* Sulzer (=*Thecla togarna* Hew., =*Thecla linus* Sulzer [H. K. Clench, pers. comm.]) (Fig. 1).

Arawacus aetolus is a particularly appropriate experimental animal for studying the "false head" hypothesis. First, it is the most frequently cited species in discussions of the hypothesis (Longstaff, 1908; Salt, 1931; Curio, 1965; Wickler, 1968; Edmunds, 1974a). Second, unlike many other Neotropical lycaenids, males of this species are relatively easy to observe. Males occupy "territories" for most of the day during good weather (see Powell [1968] and Scott [1974a] for a discussion of this behavior), do not leave their "territory" even when

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Fig. 1. Male of the Neotropical lycaenid, *Arawacus aetolus*. Notice the convergent dark-colored bands and white-tipped tails. I used the second dark-colored band (arrow) to measure the angle at which these butterflies land (see text).

disturbed repeatedly, and land within two meters of the ground. Third, *A. aetolus* is relatively common throughout the year in Gamboa, Republic of Panama, where I did this work.

This paper consists of two sections. The first part is an historical review and commentary on the components of lycaenid wing patterns and behaviors which hypothetically contribute to an impression of a head. Although descriptions of wing pattern components are straightforward, previous descriptions of three "false head" behaviors and of the circumstances under which they occur were sometimes contradictory. Thus, I augment this review with recent data on lycaenid behavior, particularly quantitative descriptions of the behavior of *A. aetolus*. The second part of the paper is an examination of the evidence supporting the "false head" hypothesis. I discuss the use of wing damage as indirect evidence of unsuccessful predator attacks, and the ways in which it can be used to test the "false head" hypoth-

esis. Finally, I summarize observations of predators attacking lycaenids under field conditions.

DEVELOPMENT OF THE HYPOTHESIS

Wing Pattern Components

A number of biologists (Kirby & Spence, 1818; Trimen, 1887; Poulton, 1890, 1902 & included references; Bell, 1906; Burn, 1906; Longstaff, 1905, 1906; Sibree, 1915; Mortensen, 1918; and Salt, 1931) have independently noted that the tails and spot of color at the anal angle of most lycaenid butterflies resemble antennae and eyespots, respectively (Fig. 1). The impression of a head is further strengthened by other aspects of wing pattern and morphology: 1) The anal angle is frequently everted at right angles to the wings so that the "head" has a three-dimensional appearance, particularly when viewed from above; 2) The tails are crossed so that they "flicker" when the hindwings are moved in a sagittal plane, and are white-tipped so that they are more conspicuous than the stationary real antennae; 3) The wings of some species have conspicuous lines converging (and presumably leading a predator's eye) towards the anal angle (Fig. 1). Although specimens illustrating the "false head" hypothesis in popular books have all of these characters, the number of such characters possessed by any one species varies considerably.

Several authors (Poulton, 1890; Bell, 1906; Burn, 1906; Sibree, 1915; Mortensen, 1918; Collenette, 1922) stated that the anal angle of lycaenid hindwings should break off if grabbed by a predator, so an attacked butterfly can escape (a situation analogous to lizards which autotomize their tails when grabbed). Van Someren (1922) confirmed that the anal angle of lycaenids breaks off when a lizard grabs it, and that the butterfly escapes unharmed. It is likely, therefore, that an enlarged or elongated anal angle area would be advantageous to the butterfly, and may be the adaptive significance of the angular hindwing shapes of many lycaenids, particularly "hairstreaks" (Theclinae).

Marshall (1902) and Van Someren (1922) suggested that the anal angle of lycaenid butterflies is an area of attraction to visual predators rather than a "false head." The primary evidence supporting this view is that the tails of some species do not resemble antennae. Although this argument is reasonable, these alternate views predict the same behavior by a predator, and cannot be distinguished.

Behavioral Components

One proposed "false head" behavior of lycaenid butterflies is moving their hindwings alternately back and forth along the cephalic-

caudal axis while resting. Trimen (1862–1866) and Niceville (1890) believed that all lycaenids move their hindwings, and there are records for species of Theclinae ("hairstreaks") (e.g. Swainson, 1821–1822; Wallace, 1853; Belt, 1874; and Planter, 1903), Polyommatinae ("blues") (e.g. Bell, 1906; Longstaff, 1908), and Lycaeninae ("coppers") (e.g. Scott, 1974b) (see Eliot [1973] for taxonomy). However, not all species in these groups move their hindwings (e.g. *Lycaena phlaeas* L. in New England, pers. obs.). Also, observations in other lycaenid subfamilies (Lipteninae, Poritiinae, Liphyrinae, Miletinae, and Curetinae) do not explicitly mention whether this behavior occurs (Poulton, 1918). I have watched more than 100 Neotropical species of the closely related family, Riodinidae, and have never seen hindwing movements (although the tails of some species are blown by the wind).

The function of hindwing movements is generally interpreted as attracting the attention of predators to the "false head" (Trimen, 1887; Poulton, 1890; Mortensen, 1918; Salt, 1931; Curio, 1965), but there are two problems with this interpretation. First, tailless species lacking conspicuous spots at the anal angle also move their hindwings (Poulton, 1918; Klots, 1951). Poulton (1918) suggested that "the movements now observed in tailless Lycaenids had persisted from some ancestral time when tails were present" and perhaps secondarily direct attention to patterns on the hindwing margins. However, it might be advantageous for a butterfly to draw a predator's attention to its hindwings whether or not the insect had a "false head."

A second problem of interpretation is that hindwing movements occur sporadically. Poulton (1918) observed hindwing movements of *Satyrium w-album* Knoch. (=*Thecla w-album*) during "short rests, generally on flowers, between flights in hot sun." Perkins (1918) corroborated this observation, but Mortensen (1918, 1919) observed no hindwing movements under similar conditions. Further, Poulton (1919) and Perkins (1919) noted that *Celastrina argiolus* L. (=*Cyaniris argiolus*) may move their hindwings during long (10-minute) rests. I have observed lycaenid butterflies occasionally moving their hindwings while walking (*A. aetolus*), while ovipositing (*Celastrina pseudargiolus* B. & L., *Incisalia augustinus* Westwood, *Strymon basilides* Geyer, and *A. aetolus*), and while apparently basking in the sun (*I. augustinus*, *Satyrium calanus* Hbn.). If hindwing movements attract the attention of predators, and I believe that they do, it remains to be shown that their sporadic and seemingly unpredictable occurrence is advantageous.

Other possible functions of hindwing movements are that the "rubbing" of the wings produces sounds or disperses pheromones. Swin-

ton (1878) suggested that the anal vein of the ventral forewing is a stridulating organ. Scudder (1889) rejected this suggestion, but described a patch of scales on the inner margin of lycaenids which might function similarly. Evidence for pheromone dispersal is that males of many species have specialized "scent" scales where the wings overlap (Eliot, 1973). However, hindwing movements have not been noted to occur during courtship (Powell, 1968; Gorelick, 1971; Scott, 1974b; Lundgren & Bergstrom, 1975; pers. obs. of *C. pseudargiolus*, *I. augustinus*, *Strymon melinus* Hbn., *Satyrium edwardsii* Saunders, *Theritas mavors* Hbn., and *A. aetolus*), and it is unlikely that any sounds or pheromones produced by hindwing movements function during courtship.

A second behavior which presumably enhances deceptiveness of lycaenid butterflies is landing head-downwards. Observations of this behavior have been contradictory, perhaps because few species land on vertical substrates, such as tree trunks, on which head position can be unequivocally recorded. Longstaff (1906, 1908) and Collenette (1922) noted head-downwards resting postures, with few exceptions, among lycaenids in England, Jamaica, Trinidad, South Africa, Ceylon, and Malaya. On the other hand, Mortensen (1918) reported that Panamanian lycaenids land horizontally. Further, Johnson & Borgo (1976) recorded the resting postures of males of *Callophrys gryneus* Hbn. perching on red cedar (*Juniperus virginiana*) as "head up," "horizontal," or "head down," and found no statistical difference in the frequency of "head up" and "head down" positions. Butterflies do not land exactly horizontally, of course, and the "horizontal" of one author may have been the "head-downwards" of another.

I measured the angle of inclination at landing (with respect to the horizontal) of *A. aetolus* males, which normally land on "horizontal" leaves, and *S. basilides* males, which often land on tree trunks and other vertical surfaces, as a preliminary attempt to resolve these conflicting reports with quantitative data. I measured this angle to the nearest degree for 211 landings of 11 individuals of *A. aetolus* (Fig. 2) with a Brunton compass using the second discal black band on the ventral wing surfaces (Fig. 1) as the butterfly's "horizontal axis." I calculated a mean angle of 7.0° downwards, s = 21.42°, and a 95% confidence interval for the mean angle of 9.9° downwards to 4.1° downwards. The probability that the parametric mean is 0° (horizontal) or upwards is less than 0.001. Thus, there is a statistical bias towards landing head-downwards in *A. aetolus*. I also observed 50 landings of *S. basilides* during which the butterflies landed at right angles to the ground with their head downwards 47 times. The other three times, the butterfly landed at an acute angle to the perpendicular, and
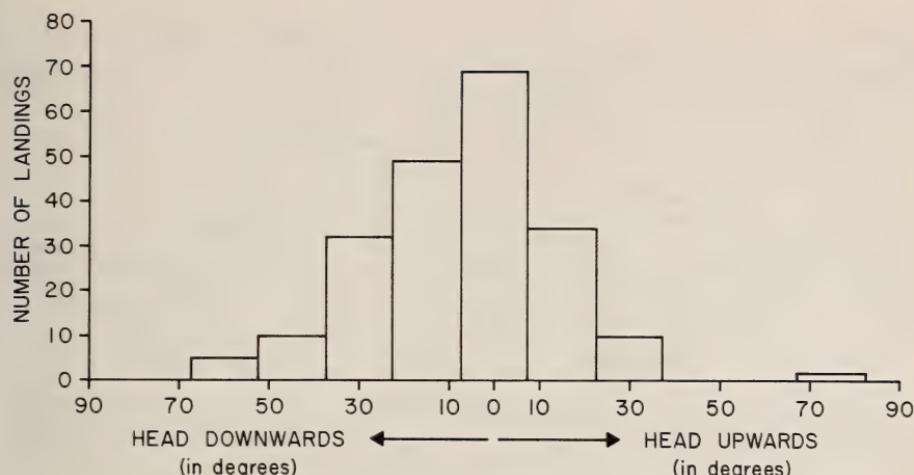
FIG. 2. The angle of inclination (with respect to the horizontal) upon landing of males of *A. aetolus*. The mean angle is 7.0° downwards with a standard deviation of 21.42° (n = 211).

immediately turned head downwards. If the resting postures of *S. basilides*, *A. aetolus*, and *C. gryneus* are indicative of other lycaenids, I tentatively conclude that lycaenids which rest on vertical surfaces land head-downwards, lycaenids which rest on broad leaves land head-downwards "on average," and lycaenids which rest on the scale-like foliage of some gymnosperms show no statistical preference for head-downwards or head-upwards.

Although lycaenids tend to land head-downwards, the advantage of this behavior for butterflies with "false head" wing patterns is obscure. Longstaff (1905, 1906) stated that the resemblance of a "false head" to a real head would be more "striking if . . . Lycaenids . . . habitually rest with the head downwards," but stated no explicit reasons for this proposal. He (Longstaff, 1908) reported proposals of Sidgwick that a butterfly which rests "head downwards is less conspicuous than one in the opposite position" and of Marshall that "the head-down position gives the insect a much better opportunity of launching into a rapid flight, and thus evading attack . . . ." Neither of these proposals, however, explains how landing head-downwards would increase the resemblance of a "false head" to a real head. Later authors (e.g. Nicholson, 1927; Wickler, 1968) suggested that most butterflies rest head-upwards, and as a result, predators would be likely to attack the posterior end of lycaenids which rest head-downwards. Evidence indicates, however, that most butterflies, like lycaenids, rest head-downwards: Longstaff (1908) and Marshall (cited in Longstaff,
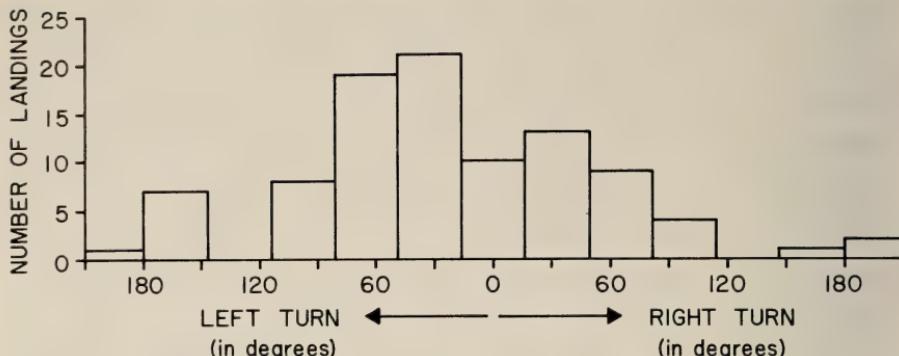
FIG. 3. The angle through which males of *A. aetolus* turned within five seconds of landing. Landings on which a male did not turn are not recorded. The mean angle turned is 19.1° left with a standard deviation of 83.25° (n = 95).

1908) noted that nymphalids (with the exception of the Danaidae and Acraeidae) land head-downwards; in Panama, all nymphalids (e.g. *Prepona, Historis, Catagramma, Colobura, Hamadryas*) and riodinids (e.g. *Thisbe lycorias* Hew., *Calociasma lilina* Btlr.) which I observed on vertical surfaces also rested head-downwards. Further, I did not see any species which consistently rested head-upwards. A predator, then, would not "expect" a lycaenid to be resting head-upwards, and landing head-downwards probably should be removed from the repertoire of presumed "false head" behaviors.

A third behavior which hypothetically enhances the deceptiveness of lycaenid butterflies is turning around immediately upon landing. This behavior has been noted in *Talicada nyseus* Guer. (Longstaff, 1906), *A. aetolus* (Curio, 1965), and *Atlides halesus* Cr. (Winkler, 1977). Curio suggested that turning around upon landing might deceive a visually-hunting predator which saw the direction in which the butterfly landed. I observed 231 landings of 17 males of *A. aetolus* to more accurately describe this behavior. On 131 (58%) occasions, the individual did not turn within 5 sec of landing. I measured the angle and direction through which the butterfly did turn in the other 95 (42%) landings using a hand-held protractor (Fig. 3). There is a curious bias towards turning to the left, which is illustrated by the mean angle turned (19.1° left from initial landing position) and a 95% confidence interval for this mean (36.1° left to 2.2° left). I also found that turning may occur after long rests, when an object such as a camera lens is moved towards the butterfly's real head, when a walking butterfly reaches the edge of a leaf, or while a female is looking for an oviposition site on a leaf or stem of its larval foodplant. Indi-

viduals of other species, however, such as S. *basilides*, turn around infrequently (less than 10% of the times they land). If turning around upon landing is deceptive, then the variance in frequency of this behavior must be explained.

TESTING THE "FALSE HEAD" HYPOTHESIS

There are three proposed mechanisms by which a "false head" at the posterior end of a lycaenid might provide protection from predators. First, Kirby & Spence (1818), Trimen (1887), and Bell (1906) suggested that "false head" wing patterns alarm or menace potential predators. This hypothesis is probably not true for mantids (Burn, 1906), and is clearly not true for lizards (Van Someren, 1922) which preferentially direct their attacks towards the "false head" of lycaenids. Second, Kirby & Spence (1818) and Poulton (1890) suggested that the apparent presence of two heads confuses potential predators. Once again, the directed attack of lizards towards the "false head" falsifies this hypothesis, at least for the species Van Someren observed. There are some Neotropical species, however, which have an "eyespot" at the base of the hindwings (near the thorax), as well as a "false head" (e.g. *Rekoa meton* Cr., "*Thecla*" *atesa* Hew., *Atlides inachus* Cr.), and it is possible that such wing patterns confuse predators. A third suggestion is that "false head" wing patterns deflect predator attacks towards the less vulnerable posterior end of the butterfly. I devote the remainder of this paper to a discussion of the evidence bearing on this last hypothesis.

Hindwing Damage by Predators

A number of authors (Poulton, 1902 & included references; Burn, 1906; Longstaff, 1906; Collenette, 1922) considered lycaenid butterflies with the anal angle (or adjacent areas) of both hindwings broken off (Fig. 4) to be indirect evidence of a predator's unsuccessful attack directed at the "false head." Three lines of evidence support this proposal. First, Van Someren (1922) confirmed that the unsuccessful attacks of lizards produce this kind of wing damage. Second, I marked individuals of A. *aetolus* using felt-tip markers, and monitored them under field conditions for several weeks to determine whether symmetrically missing pieces of hindwing can result from gradual wear. I found that hindwing margins gradually frayed with age, rather than breaking cleanly to produce the symmetrical damage shown in Fig. 4. Third, I confined six A. *aetolus* females in net bags (for an average of three days each) over plants with recurved spines on branches and both leaf surfaces (*Solanum lancaeifolium*) to determine whether sharp objects, such as thorns, might cause symmetric gaps in hind-
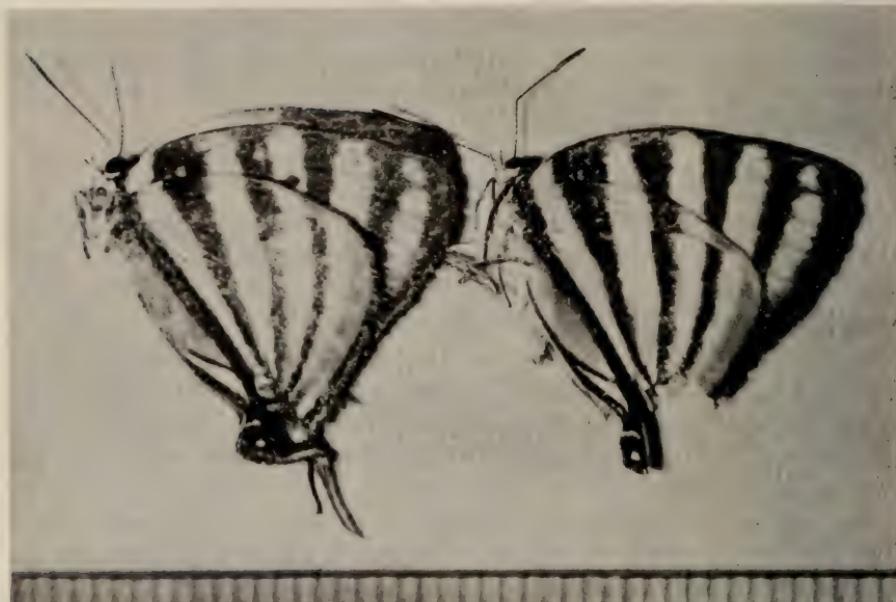
FIG. 4.   Individuals of *A. aetolus* before and after sustaining symmetrical hindwing damage. Individual on the right had no damage to its hindwings four days prior to its capture. Scale in mm.

wing margins. Although wing margins of these individuals frayed rapidly, as is usually the case with butterflies confined by net bags, I found no symmetrical damage. Thus, I conclude that the rate at which lycaenid butterflies sustain symmetrical damage to their hindwings is a relative measure of the frequency of unsuccessful predator attacks.

The following "baseline data" are reported for frequencies of symmetrical hindwing damage. Collenette (1922) reported that the percentage of lycaenid specimens in Malaya with symmetrical hindwing damage was as high as 10% in worn specimens. Robbins (1978) found 7.9% (n = 1024) of hairstreak butterfly specimens (Eumaeini) from Villavicencio, Meta, Colombia, and 7.0% (n = 386) of such specimens from the Republic of Panama with such hindwing damage. Such data are easy to collect, but have the disadvantage of being dependent on lifespans since old individuals are more likely to have sustained wing damage than young ones (Edmunds, 1974b). As an alternative, I estimated the rate at which individuals of *A. aetolus* sustain hindwing damage. Each time I re-sighted a marked individual of *A. aetolus*, I recorded the number of days since the previous sighting and whether hindwing damage had been sustained since that previous sighting (Table 1). From these data, I estimate (see Appendix) a 2.7% proba-

TABLE 1. The number of marked individuals of *Arawacus aetolus* with and without new hindwing damage (since the previous sighting) as a function of the number of days since that previous sighting. The number of days since the previous sighting was omitted from the table if there were no individuals found after that interval of days. From these data, I estimated the probability that an individual sustained wing damage was 2.7% per day.

No. of days since previous sighting	No. of sightings with no wing damage	No. of sightings with wing damage	Total no. of sightings
1	18	0	18
2	12	0	12
3	6	1	7
4	7	1	8
5	1	0	1
6	2	0	2
7	2	0	2
9	0	1	1
14	0	1	1
17	1	0	1
19	1	0	1
20	0	1	1
30	1	0	1
34	0	1	1

bility of sustaining hindwing damage per day for surviving individuals of *A. aetolus*. Although these data are too scanty to test the assumptions of the model (Appendix) or to reasonably estimate a variance for this probability, this figure is probably a good first estimate of the true rate at which individuals of *A. aetolus* sustain wing damage. In addition, this method might be used profitably on locally abundant species for which larger sample sizes could be collected. I emphasize, however, that frequency of hindwing damage is a relative measure of unsuccessful predator attacks, and not of successful ones (for which one first would have to make assumptions such as age-independent mortality).

Tests of Deflected Attacks by Predators

One way to test whether "false head" wing patterns deflect predator attacks is to compare the frequency of specimens with damage at their anal angle to the frequency of specimens with damage to other parts of the wings. If "false head" wing patterns do deflect predator attacks, then the frequency of predator-inflicted damage should be greatest at the "false head." Such a comparison assumes that the wings of lycaenid butterflies will break off wherever grabbed. To test this assumption, I measured the force needed to break different parts of lycaenid wings using an artificial "beak" apparatus (Fig. 5). I found
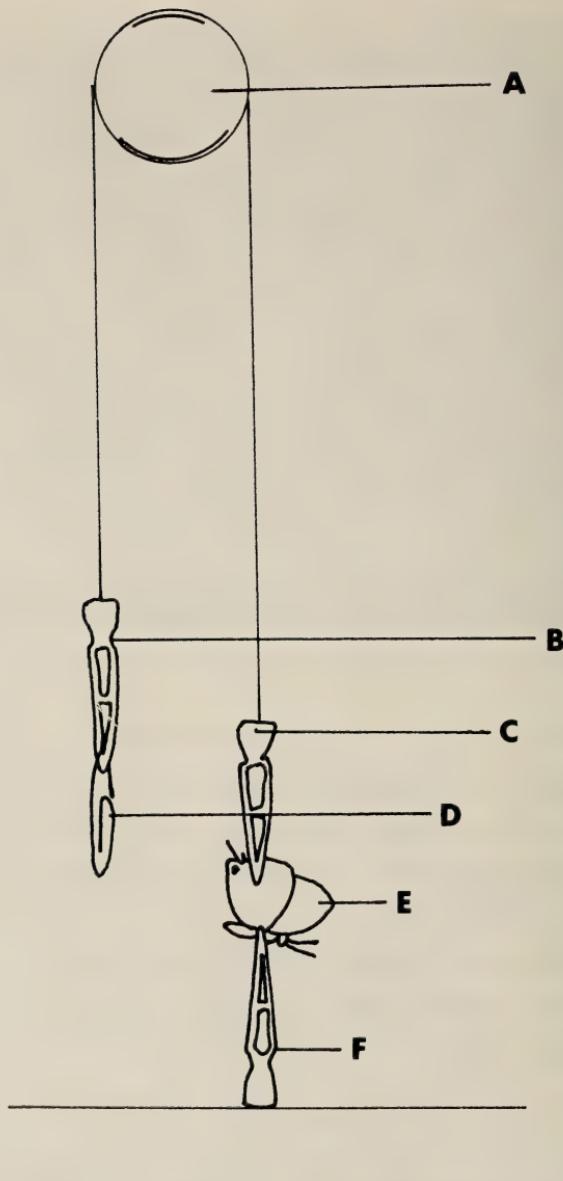
FIG. 5. Artificial "beak" apparatus. a, pulley; b, hair pin; c, hair pin used as a beak; d, paper clip weights; e, butterfly; f, attachment to butterfly. The force needed to break part of the wings being tested was measured by the weight of paper clips needed to break the wings. Scale line (lower left) = 2 cm.

that the outer margins of both wings and the hindwings adjacent to the anal angle break the most easily, while the forewing costal vein and the area where all four wings overlap are the most resistant to breakage (more than four times stronger than the anal angle area). These results are corroborated by the incidence of beak marks (impressions of beaks on butterfly wing surfaces) on lycaenid butterflies. The majority of beak-marked individuals which I have seen had been grabbed by all four wings or across the forewing costal vein. This result indicates that wings do not break when grabbed in these areas. Thus, frequencies of predator-inflicted wing damage to different areas of the wings cannot be used to test the "false head" hypothesis. However, these results also indicate that, in terms of probability of escape, it is most advantageous for the butterfly to be grabbed at its "false head."

A second way to test whether "false head" wing patterns deflect predator attacks is to compare the predicted and observed deceptiveness of a wide range of lycaenid wing patterns. If "false head" wing patterns do deflect predator attacks, then species possessing more of the proposed components of "false head" wing patterns should have a higher frequency of predator-inflicted hindwing damage. I made such a comparison (Robbins, 1978; 1980), and the results were consistent with those predicted by the "false head" hypothesis. This test also raises the question of why, if some "false head" wing patterns are particularly deceptive, all species have not evolved these wing patterns.

A third, more direct way to test whether "false head" wing patterns deflect predator attacks is to watch how predators attack lycaenid butterflies. Such systems are difficult, at best, to set up in the lab (e.g. Collenette 1922), and there is only one report of predators attacking lycaenids under field conditions. In a remarkable, yet little known paper, Van Someren (1922) reported his observations of lizards attacking lycaenids. He found that lizards invariably attacked the posterior end of these insects, and did not attack when the real head of the butterfly was closest to the lizard. Further, Van Someren reported that lizards were successful only if they grabbed part of the butterfly's body; otherwise they got a piece of hindwing, and the butterfly flew off. Thus, Van Someren confirmed that the "false head" of a lycaenid butterfly can deflect predator attacks to its posterior end, and as a result, the butterfly may escape unharmed.

LITERATURE CITED

BELL, T. R. 1906. Observations on Indian butterflies. Entomol. Monthly Mag. 42: 121–128.

BELT, T. 1874. The naturalist in Nicaragua. John Murray, London. 403 p.

BURN, G. H. 1906. No title. Proc. Entomol. Soc. Lond. 1906: lii.

COLLENETTE, C. L. 1922. Protective devices by lycaenid butterflies against the attacks of lizards and birds. Journal Straits Branch, Royal Asiatic Society 85: 230–231.

COTT, H. B. 1940. Adaptive colouration in animals. Methuen, London. 508 p.

CURIO, E. 1965. Ein Falter mit "falshem Kopf." Natur und Museum 95: 43–46.

D'ABRERA, B. 1971. Butterflies of the Australian region. Lansdowne, Melbourne. 415 p.

EDMUNDS, M. 1974a. Defence in animals. A survey of anti-predator defences. Longman, Essex. 357 p.

———. 1974b. Significance of beak marks on butterfly wings. Oikos 25: 117–118.

ELIOT, J. N. 1973. The higher classification of the Lycaenidae (Lepidoptera): A tentative arrangement. Bull. Brit. Mus. (Nat. Hist.) Entomol. 28: 6.

GORELICK, G. A. 1971. A biosystematic study of two species of Callophrys (Callophrys) in California (Lycaenidae). J. Lepid. Soc. 25, Suppl. 2.

JOHNSON, K. & P. M. BORGO. 1976. Patterned perching in two Callophrys (Mitoura) (Lycaenidae). J. Lepid. Soc. 30: 169–183.

KIRBY, W. & W. SPENCE. 1818. An introduction to entomology or elements of the natural history of insects. Longman, Hurst, Rees, Orme, and Brown. 2nd ed., vol. 2, 530 p.

KLOTS, A. B. 1951. A field guide to the butterflies of North America, east of the Great Plains. Houghton Mifflin, Boston. 349 p.

LONGSTAFF, G. B. 1905. Notes on the butterflies observed in a tour through India and Ceylon. 1903–1904. Trans. Entomol. Soc. Lond. 1905: 61–144.

———. 1906. Some rest-attitudes of butterflies. Trans. Entomol. Soc. Lond. 1906: 97–118.

———. 1908. Bionomic notes on butterflies. Trans. Entomol. Soc. Lond. 1908: 607–673.

LUNDGREN, L. & G. BERGSTOM. 1975. Wing scents and scent-released phases in the courtship behavior of Lyciades argyrognomon (Lepidoptera: Lycaenidae). J. Chem. Ecol. 1: 399–412.

MARSHALL, G. A. K. 1902. The bionomics of South African insects. Trans. Entomol. Soc. Lond. 1902: 287–585.

MORTENSEN, T. 1918. Papers from Dr. Th. Mortensen's Pacific expedition. 1914–1916. I. Observations on protective adaptations and habits, mainly in marine animals. Vidensk. Medd. Dansk Naturhist. Foren. Kjøbenhavn 69: 57–96.

———. 1919. No title. Proc. Entomol. Soc. Lond. 1919: xi–xii.

NICEVILLE, L. DE. 1890. The butterflies of India, Burmah and Ceylon, vol. III. Calcutta Central Press, Calcutta. 503 p.

NICHOLSON, A. J. 1927. A new theory of mimicry in insects. Australian Zoologist 5: 10–104.

OWEN, D. F. 1971. Tropical butterflies. The ecology and behaviour of butterflies in the tropics with special reference to African species. Clarendon Press, Oxford. 214 p.

PERKINS, R. C. L. 1918. No title. Proc. Entomol. Soc. Lond. 1918: xlvi–xlvii.

———. 1919. The eccentric movements of the hind-wings in *Cyaniris argiolus* L. Proc. Entomol. Soc. Lond. 1919: xi.

POULTON, E. B. 1890. The colours of animals. The International Scientific Series, vol. 67. D. Appleton, New York. 360 p.

———. 1902. Signed sections in Marshall (1902).

———. 1918. No title. Proc. Entomol. Soc. Lond. 1918: xlvi–xlviii.

———. 1919. No title. Proc. Entomol. Soc. Lond. 1919: xi.

PLANTER, E. A. 1903. Mimicry as observed in Egypt. The field, the farm, the garden. 101: 40.

POWELL, J. A. 1968. A study of area occupation and mating behavior in *Incisalia iroides*. J. New York Entomol. Soc. 76: 47–57.

ROBBINS, R. K. 1978. Behavioral ecology and evolution of hairstreak butterflies (Lepidoptera: Lycaenidae). Tufts University, Medford, Mass. 146 p. Dissertation.

———. 1980. The "false head" hypothesis: predation and wing pattern variation of lycaenid butterflies. Am. Nat., in press.

SALT, G. 1931. The "false head" of many Colombian lycaenid butterflies. Proc. R. Entomol. Soc. Lond. 6: 19–22.

SCOTT, J. A. 1974a. Mate-locating behavior of butterflies. Amer. Midl. Natur. 91: 103–117.

———. 1974b. Population biology and adult behavior of *Lycaena arota* (Lycaenidae). J. Lepid. Soc. 28: 64–72.

SCUDDER, S. H. 1889. The butterflies of the eastern United States and Canada with special reference to New England, vol. II. Published by the author. 1774 p.

SIBREE, J. 1915. Naturalist in Madagascar. Cited in: Another independent observation of the "false head" in butterflies. Proc. Entomol. Soc. Lond. 1917: lxv.

SWAINSON, W. 1821–1822. Zoological illustrations. 1st series, vol. II. Baldwin, Cradock, and Joy, Paternoster-Row; and W. Wood, Strand., London. Plates 67–119 (unpaginated).

SWINTON, A. H. 1878. On the implied power of stridulation in the hair-streak butterflies (*Thecla*). Entomol. Monthly Mag. 14: 209–210.

TRIMEN, R. 1862–1866. Rhopalocera Africae Australis. Truber, London. 353 p.

———. 1887. South African butterflies, vol. 1. Truber, London. 355 p.

VAN SOMEREN, V. G. L. 1922. Notes on certain colour patterns in Lycaenidae. J. of E. Africa and Uganda Nat. Hist. Soc. 17: 18–21.

WALLACE, A. R. 1853. On the habits of the butterflies of the Amazon Valley. Trans. Entomol. Soc. Lond., new series 2: 253–264.

WICKLER, W. 1968. Mimicry in plants and animals. McGraw-Hill, New York. 255 p.

WINKLER, V. T. 1977. Ein Zipfelfalter (*Atlides halesus* Cramer 1779) mit Pseudokopf (Lepidoptera: Lycaenidae, Theclinae). Zool. Anz. Jena 198: 31–35.

APPENDIX

The following model can be used to estimate the rate per day at which surviving butterfly individuals sustain symmetrical hindwing damage. It assumes that this rate is age-independent, an assumption which is probably accurate except for very old individuals. This model is unlikely to be original, but I have been unable to find it published elsewhere.

Let u be the probability that a butterfly survives and does not sustain hindwing damage within one day.

$p(i)$ be the probability that a sighted, marked individual was last sighted i days ago.

$N(i)$ be the number of individuals sampled which were re-sighted after i days.

$n(i)$ be the number of individuals sampled which were re-sighted after i days and which had no new hindwing damage since the last sighting.

The probability of re-sighting an individual after i days with no new wing damage is $p(i)u^i$ and the probability with wing damage is $p(i)(1 - u^i)$.

The log-likelihood equation is

$$\ln(L) = \sum [N(i)\ln(p(i)) + n(i)\ln(u^i) + (N(i) - n(i))\ln(1 - u^i)]$$

Taking the partial derivative with respect to u, and setting it equal to zero yields the following equation for u^*, the maximum likelihood estimate of u.

$$\sum \frac{iN(i)u^{*i} - in(i)}{(1 - u^{*i})} = 0$$

This equation can be solved numerically for u^*, and the maximum likelihood estimate of $(1 - u)$ is $(1 - u^*)$. With sufficient data and with estimates for the $p(i)$, this model can be tested by a goodness of fit test.

A REVIEW OF THE *ERORA LAETA* GROUP, WITH DESCRIPTION OF A NEW SPECIES (LYCAENIDAE)

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ABSTRACT. Members of the *laeta* group of *Erora* are discussed, especially their relationships with *Erora caudata*, n. sp. (Oxchuc, Chiapas, Mexico). Superficial and genitalic comparisons are made.

In lepidopterological matters Harry Clench's greatest devotion (apart from Bahamian butterflies in general) was to the Lycaenidae of Mexico. One of his "favorite" genera was *Erora*, and he long contemplated a revision of it and its relatives. Anyone who has ever examined a specimen (especially a female) of this extraordinarily beautiful group could appreciate Harry's infatuation with *Erora*.

Since I knew of this, when the Allyn Museum obtained a pair (more were to come later) of a strange *Erora* from Chiapas, Mexico, I immediately submitted them to Clench. His almost instantaneous reply was that not only was this insect a new species of *Erora*, but it also would cause a redefinition of the genus. One of the previously accepted characteristics was that *Erora* lacked "tails" on the hindwing, a feature of the new entity. We at once settled upon an informal name for this taxon, but Harry did not live long enough to provide even a rudimentary description of it. Accordingly, I describe this lovely hairstreak and discuss its relatives within *Erora*, dedicating this paper to the memory of Harry Clench, and trusting that he would not have been disappointed in the final product.

The *Erora laeta* group comprises three "look alike" species distributed in parts of the United States, Mexico, and Guatemala. They are slate-gray (males) to black with median blue markings (females) on the upper surface; on the under surface they are conspicuously scaled with blue-green, especially the hindwings, with overlying brick-red spots or chevrons. All share genitalic similarities in both sexes. These species cannot be confused with any other group of hairstreaks; most specimens can be determined within the group by their locality labels. The two previously described species are allopatric: *E. laeta* (W. H. Edwards) is confined to the northeastern United States and adjacent Canada, whereas *E. quaderna* (Hewitson) is found in the southwestern United States and montane Mexico, perhaps as far south as the mountains of Guatemala. These two species have been figured often (see plates in Godman and Salvin (1879–

1901), Holland (1931), Klots (1951) and Howe (1975)). An adequate genitalic analysis of *laeta* and *quaderna* (with figures of both sexes) was given by Field (1941). The conclusions reached by Field (1941) are modified, usually along the lines suggested by Clench (1943), but Field's figures are adequate for the discrimination of the previously described species.

Key to the *laeta* group of *Erora*

1. With tail at end of hindwing vein Cu_2; Chiapas (perhaps Guatemala) _____
    _____ *caudata*, n. sp.
1a. Tailless _____ **2.**
2. Fringes of wings above grayish, if orange present it is faint; eastern U.S. and adjacent Canada _____ *laeta* (W. H. Edwards).
2a. Fringes of wings above conspicuously orange _____ **3.**
3. Brick-red markings of under surface of ♂ somewhat more extensive; ♀ blue areas of upper surface more restricted and violet tinted; southwestern U.S. to Sinaloa, Mexico_____ *quaderna sanfordi* dos Passos.
3a. Brick-red markings of under surface reduced in ♂; ♀ blue areas of upper surface more extensive; montane Mexico (Nuevo Leon and south) (perhaps Guatemala) _____ *quaderna quaderna* (Hewitson).

Erora caudata L. Miller, new species
Figs. 1–4

Male. Head, thorax and abdomen covered with slate-gray hairs. Antennal shaft black, ringed with narrow white bands; club black with fulvous tip and two lateral fulvous bands (the latter not readily apparent to the naked eye). Palpi black with intermingled ventral white hairs. Eyes hairy, slightly emarginate, brown to red-brown, ringed laterally and mesially with white scales. Legs bluish-white, but black ringed with white distad.

Forewing upper surface slate-gray, darkest distad; otherwise unmarked. **Hindwing** with short tail at end of Cu_2; upper surface basically slate-gray, shiny in disc of wing, with narrow, intermittent, pale shining blue submarginal line from near tornus to about M_3; slight indication of darker submarginal spots from M_1-M_2 to Cu_2-2A (some or all spots not apparent in all specimens). Fringes of both wings fulvous; brick-red fringe hairs at hindwing tornus.

Forewing under surface dull gray, but broadly blue-green at apex and along costa; postmedian band of red-brown crescents, bordered distally with white, extending from $Rs-M_1$ to Cu_1-Cu_2. **Hindwing under surface** blue-green marked with red chevrons, spots and crescents outwardly edged in white (Fig. 2); light halos of distal band almost obsolescent. Fringes of both wings fulvous, but brick-red on tail and at tornus of hindwind.

Length of forewing. Holotype ♂ 13.3 mm, seven ♂ Paratypes 11.2 to 13.5 mm, mean 12.4 mm.

♂ **genitalia** (Fig. 5) closely resemble those of *E. laeta* and *quaderna* (Field, 1941: plate II). Falces without prominent shoulders and with apex not so strongly upturned as in *laeta* (similar to *quaderna*); valvae with apex more attenuated than in either of the other two species and not so strongly recurved dorsad.

Female. Head, thorax, abdomen and appendages as in ♂.

Forewing upper surface black-brown with blue area (more violet shaded than in either *laeta* or *quaderna quaderna*, about as in *quaderna sanfordi*) restricted to basal two-thirds of wing from inner margin to posterior margin of cell and transected by black veins. Basal three-quarters of **hindwing upper surface** violaceous blue (bluer in *laeta* or *quaderna*) with veins black; margins broadly blackish-brown, narrowing
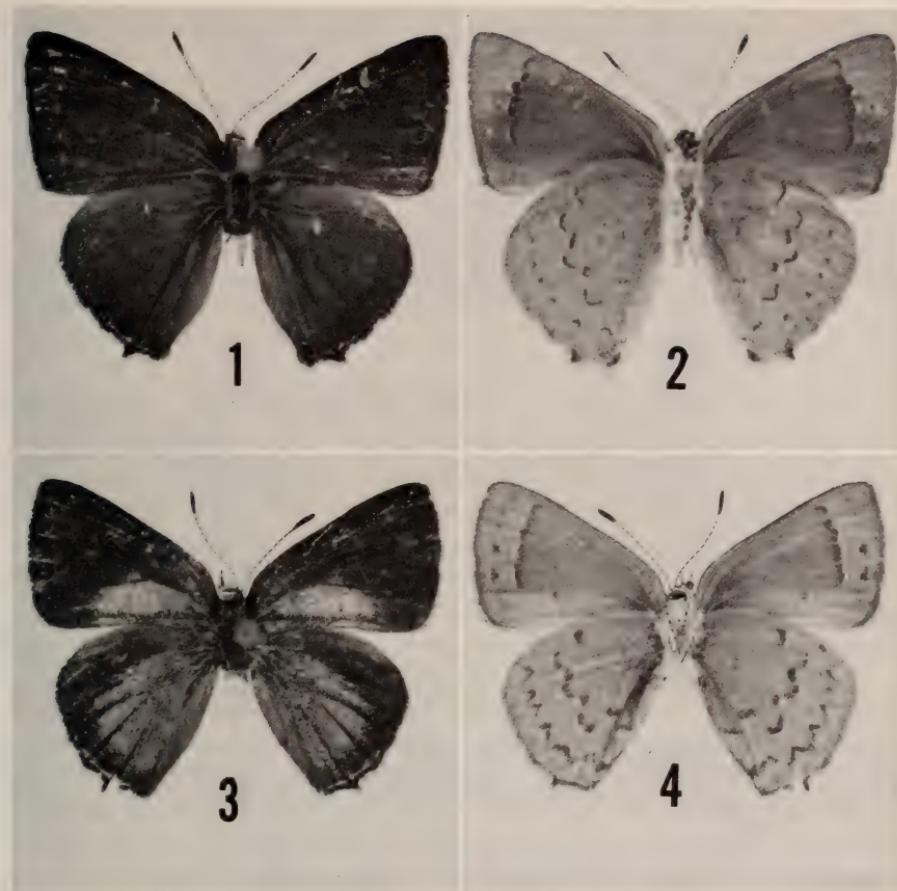
FIGS. 1–4. *Erora caudata* L. Miller, new species. **1–2.** Holotype ♂, upper (1) and under (2) surfaces; MEXICO: CHIAPAS: Ochuc (Oxchuc). **3–4.** Paratype ♀, upper (3) and under (4) surfaces; same data as Holotype. Specimens in collection of Allyn Musuem of Entomology (Allyn Museum photos Nos. 121979-15 to 18, respectively).

tornally; irregular shining blue submarginal line from tornus to near M_3. Fringes fulvous on both wings; brick-red fringe hairs at hindwing tornus and intermingled with fulvous ones on tail.

Forewing under surface light gray, but broadly blue-green costad and from apex along outer margin; postmedian band of brick-red crescents outwardly edged in white nearly coalesced from near costa to Cu_2; faint dark gray submarginal spots from near apex to $Cu_1 - Cu_2$. **Hindwing under surface** blue-green with two bands of brick-red chevrons (Fig. 4), the proximal ones distally edged in white (first and last two chevrons in proximal band offset proximally, tending to break continuity of the band; distal band of chevrons has a faint distal dusting of white scales, much more so than in other *Erora* species, which serves to emphasize the red chevrons as well as the submarginal blotches mentioned later) and faint dark gray submarginal blotches from near apex to near tornus. Fringes fulvous on both wings; brick-red fringe hairs at hindwing tornus and on tail.
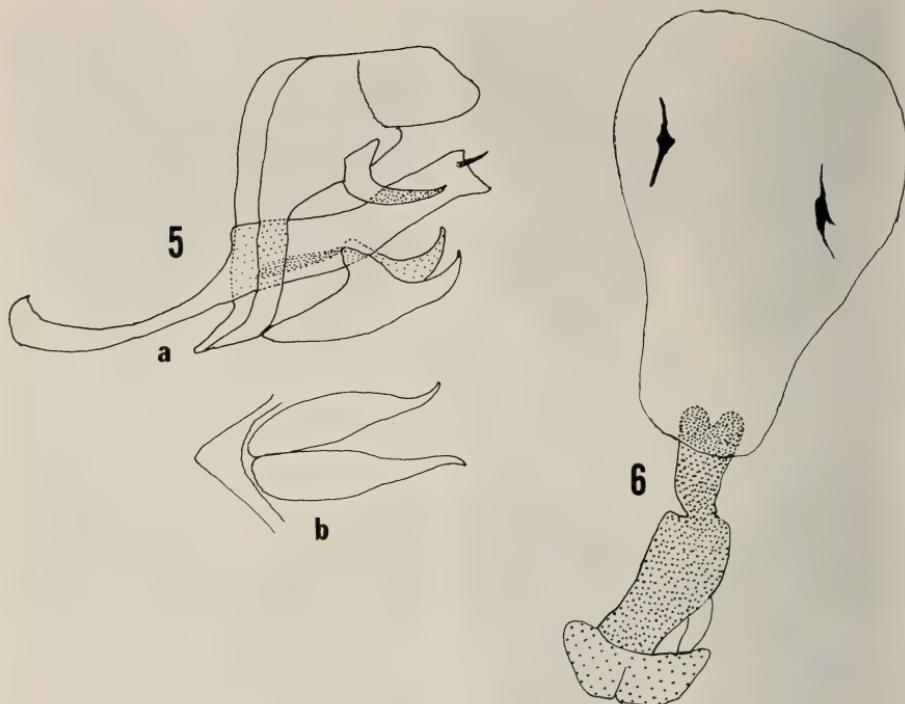
FIGS. 5–6. Genitalia of *Erora caudata* L. Miller, new species. **5.** Holotype ♂ (preparation M-3997-v, Lee D. Miller), lateral view; a), ventral view of uncus and saccus. **6.** Paratype ♀ (preparation M-3998-v, Jacqueline Y. Miller), ventral view.

Length of forewing. 10 ♀ Paratypes 10.4 to 13.5 mm, mean 12.6 mm.

♀ **genitalia** (Fig. 6) have heavily sclerotized sterigma with posterior portion only rudimentarily bifurcated (see Field, 1941: plate III for comparison with *laeta* and *quaderna*). *Caudata* resembles *quaderna* with regard to sclerotization, but the simpler sterigma belies a close relationship. The sterigma of *laeta* is much less heavily sclerotized than either of its congeners. Signa vary little among *caudata*, *quaderna* and *laeta*.

Described from 18 specimens, eight males and 10 females, from montane Chiapas, Mexico.

Holotype ♂. MEXICO: CHIAPAS: Ochuc (properly "Oxchuc"), 21–23.ix.1972 (R. G. Wind); ♂ genitalia preparation M-3997-v (Lee D. Miller).

Paratypes. same locality and collector as Holotype, various dates, 6♂ 8♀; MEXICO: CHIAPAS: Mt. Huitepec, cloud forest, 8000 ft., 15–21.vi.1975 (P. Hubbell), 1♂ 2♀.

Holotype ♂, five ♂ and eight ♀ Paratypes will remain in the collection of the Allyn Museum of Entomology; one pair of Paratypes will be deposited each in Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, and the British Museum (Natural History), London, England.

The name is feminine and refers to the presence of a tail at the end of hindwing vein Cu₂, a characteristic shared by no other member of the genus *Erora* previously described.

While the known distribution of *E. caudata* includes only Chiapas, I expect that it will be (or has been) found in adjacent Guatemala. Based on Godman's (1901, *in* Godman and Salvin, [1879–1901], vol. 2: 719) description of a specimen of *E. "quaderna"* from the Quiche Mountains of Guatemala, I am inclined to think that this specimen was *caudata*. I was unable to locate this specimen during a recent trip to the British Museum (Natural History), and until the specimen is located, the identity of the Guatemalan "*quaderna*" must remain a mystery.

Superficial characteristics alone will separate *caudata* from its congeners, especially the tailed hindwing. There are also differences in the genitalia of both sexes. I cannot, therefore, even assuming that the "*quaderna*" from Guatemala is actually a *caudata*, consider the *laeta* group as geographic segregates of a single species, though they undoubtedly are close relatives (members of a superspecies?).

Erora quaderna quaderna (Hewitson)

Thecla quaderna Hewitson, 1868: 35. Type-locality "Mexico," restricted to Tancitaro, Michoacan by Clench, 1943: 223. Holotype in British Museum (Natural History) [seen].
=*Thecla attalion* Godman and Salvin, 1887 [1879–1901], vol. 2: 60–61. Type-locality Orizaba, Veracruz, Mexico. Holotype in British Museum (Natural History) [seen].

Clench's (1943) restriction of the type-locality to Tancitaro in unfortunate, since it is unlikely that any of Hewitson's correspondents would have visited there. Other areas that harbor *quaderna* would have been better choices simply because Hewitson's collectors might have gone there, even ones relatively close to Mexico, D.F.

The male genitalia of *quaderna* (Field, 1941: plate II) have heavier upturned valves than *caudata* (Fig. 5), and have heavier valves and less elbowed falces than *laeta* (Field, 1941: plate II). The female genitalia of *quaderna* (Field, 1941: plate III) are distinguished from those of *caudata* (Fig. 6) by the deeply emarginate lamella postvaginalis; the entire sterigma is more heavily sclerotized in *quaderna* than in *laeta* (Field, 1941: plate III).

All of the specimens of *E. quaderna quaderna* that I have seen have come from the Mexican Plateau and adjacent cordillera north of the Isthmus of Tehuantepec. Specimens from Cerro Potosí, just southwest of Monterrey, Nuevo Leon, are referable to the southern subspecies, whereas material from Chihuahua and Sinaloa are not. The specimen recorded from Guatemala by Godman and Salvin (1887 [1879–1901]), as mentioned earlier, is probably a *caudata*. There seems to be no restriction of this species to cloud forest; indeed, it and its subspecies *sanfordi* are inhabitants of mesic to xeric environments where they seem to be associated with various Scrub Oaks (*Quercus*), and it is possible that at least one of these is the foodplant. The adults which I have encountered in Mexico are avid flower visitors, preferring those of a tall, yellow-flowered *Senecio* to other available blooms.

Erora quaderna sanfordi dos Passos

Erora laeta sanfordi dos Passos, 1940: 1. Type-locality White Mountains, Arizona.
    Holotype in American Museum of Natural History [seen].

This subspecies, if it is valid, is the northern representative of the Mexican *quaderna*, not *laeta* in which it was originally described (for details see Field, 1941). I have seen specimens referable to it from New Mexico, Arizona (there are also records from southern Utah) and northwestern Mexico (Madera, Chihuahua; Loberas Summit, Sinaloa). Material from northeastern Mexico is best classified as *E. q. quaderna*.

The characteristics that separate *sanfordi* from the nominate subspecies are slight and quite variable; hence, it may be necessary to compare sizable series to distinguish them. The attributes that seem to separate the two entities are summarized earlier in the key, but they are of a statistical nature. It is with some reluctance that I follow Clench (1943) and accept *sanfordi* as a subspecific name.

Erora laeta (W. H. Edwards)

Thecla laeta W. H. Edwards, 1862: 55–56. Type-locality near London, Ontario. Holotype in Carnegie Museum of Natural History [seen].
=*Thecla clothilde* W. H. Edwards, 1863: 15. Type-locality near Quebec, Quebec. Type lost (see F. M. Brown, 1970: 75 for details).

The reader is referred to F. M. Brown (1970: 74–75) for details of Edwards' confusion of the sexes of *laeta* (similar to Godman and Salvin's confusion of the sexes of *quaderna*).

E. laeta is a denizen of the Canadian and Transition zone deciduous forests of the northeastern United States and adjacent Canada. Its habitat is decidedly moister than that of *quaderna*. The southernmost records are from the mountains of northern Georgia, and specimens have been taken from as far west as the northern part of the lower peninsula of Michigan. It is primarily an Appalachian (and Laurentian) insect, and is associated with Beech (*Fagus*) woodlands. On the rare occasions that it is found commonly (a relative term, since these butterflies are never abudant), it seems to be attracted to flowers, at least to a limited degree.

Thus far little, if anything, has been published on the early stages of any of these butterlies (indeed, on any *Erora*), and some well-documented life history work on these hairstreaks would be most welcome.

The approximate distribution of the *laeta* group hairstreaks is given in Fig. 7. The captures of *Erora*, other than *laeta*, probably more closely resemble the distribution of hairstreak collectors who have

FIG. 7. Approximate distribution of members of the *Erora laeta* group. Vertical lines: *E. laeta*. Horizontal lines: *E. quaderna sanfordi*. Cross hatching: *E. quaderna quaderna*. Heavy stippling: *E. caudata*. The specimen of *E. "quaderna"* mentioned in text as probably *E. caudata* is denoted by a "?" in Guatemala. The ranges are not definitive: additional records may significantly expand known distributions, and since the beasts are very local, they do not occur everywhere within an indicated area.

ventured into the mountains of the southwestern United States, Mexico and Guatemala than of the butterflies themselves.

It is next to impossible to ascertain which of these insects is nearer the ancestral condition, but I suspect (based on the tailed condition,

characteristics cited of the male and female genitalia, *etc.*) that *cau-data* may be the more "primitive" member of the group. The lightly sclerotized female genitalia of *laeta* suggest its position as most "derived," but the possibility exists that all three species may have been derived about equally from a common ancestor.

Literature Cited

BROWN, F. M. 1970. The types of lycaenid butterflies described by William Henry Edwards. Part II—Theclinae and Strymoninae. Trans. American Ent. Soc. 96: 19–77.

CLENCH, H. K. 1943. A note on the Arizona *Erora* (Lepidoptera, Lycaenidae). J. New York Ent. Soc. 51: 221–223.

EDWARDS, W. H. 1862. Descriptions of certain species of diurnal Lepidoptera found within the limits of the United States and British America, No. 2. Proc. Acad. Nat. Sci. Philadelphia 14: 54–58.

——— 1863. Descriptions of certain species of diurnal Lepidoptera found within the limits of the United States and British America, No. 1. Trans. Ent. Soc. Philadelphia 2: 14–22.

FIELD, W. D. 1941. Notes on *Erora laeta* (Edwards) and *Erora quaderna* (Hewitson) (Lepidoptera, Lycaenidae). Ann. Ent. Soc. America 34: 303–316.

GODMAN, F. D. & O. SALVIN. 1879–1901. Biologia Centrali-Americana, Lepidoptera-Rhopalocera, 3 vols. London, Van Voorst.

HEWITSON, W. C. 1868. Descriptions of new species of Lycaenidae. London, priv. publ., 36 p.

HOLLAND, W. J. 1931. The butterfly book (rev. ed.). Garden City, N.Y., Doubleday, Doran and Co.: vii–xii + 424 pp.

HOWE, W. H. (ED.) 1975. The butterflies of North America. Garden City, N.Y., Doubleday and Co., vii–xiii + 633 p.

KLOTS, A. B. 1951. A field guide to the butterflies of North America, east of the Great Plains. Boston, Houghton Mifflin Co., vii–xvi + 349 p.

DOS PASSOS, C. F. 1940. A new subspecies of *Erora laeta* Edw. from Arizona and New Mexico. American Mus. Novitates (1052): 2 p.

FIELD NOTES ON TWO HAIRSTREAKS FROM NEW MEXICO WITH DESCRIPTION OF A NEW SUBSPECIES (LYCAENIDAE)

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ABSTRACT. Field notes are provided for two hairstreak species found in the Organ Mountains of New Mexico. A new subspecies of *Fixsenia polingi* (Barnes & Benjamin) is described.

Although he worked with many butterfly families, Harry Clench was perhaps best known to many lepidopterists for his work with the Lycaenidae. Although his most recent field trips were to the Bahamas, Harry traveled and collected in the southwestern U.S., and especially in New Mexico. In recognition of this aspect of Harry's contributions, this paper is devoted to a discussion of two hairstreaks found during 1979 in the Organ Mountains of New Mexico.

In May and June 1979, Richard Holland and I collected extensively in the Organ Mts. in Doña Ana Co. This relatively small range is oriented north-south and lies just to the east of Las Cruces. U.S. Hwy. 70 from Las Cruces to Alamogordo is the only paved-road access to the mountains, where it crosses their northern end via San Augustin Pass. On the northeastern side, there is public access to the Aguirre Spring Recreation Site, operated by the Bureau of Land Management (BLM). It is located on the desert at the base of the range. The remainder of the eastern slope is part of the White Sands Missile Range (WSMR) facility. Access is only by special permit, and limited to certain areas. The foothills of the western slope are partially BLM land and partially privately owned. There are primitive access roads to some of the canyon mouths. A hiking trail extends from Aguirre Spring across Baylor Pass to a BLM gravel access road on the west side of the range. The Pine Tree Trail is a loop trail from Aguirre Spring into the hills above the recreation site. The major south-central portion of the mountains is part of the Ft. Bliss Military Reservation and is closed to public access, although there are no barricades or signs, depending upon where one hikes.

The Organ Mts. are one of numerous isolated desert mountain ranges found in the southwestern U.S. They were formed by an upwelling of molten rock within the earth's crust—a process called mon-

zonite intrusion. Subsequent erosion of the overlying crust has left rock spires that resemble organ pipes, giving rise to their name.

Vegetation varies widely from typical southwestern desert forms (*Celtis* sp. and *Ungnadia speciosa* Endl., in the arroyos; *Prosopis* elsewhere) at the base of the range, through an oak chaparral belt to a limited coniferous forest (Douglas Fir) at the highest elevations (2590–2745 m). There is some permanent water in the interior canyons.

Considering the geographic isolation of these mountains and the apparent lack of moisture, they harbor an exceptional number of butterfly species. Many records were obtained by the author and R. Holland. A full species list will be published elsewhere by Holland.

Fig. 1 shows most of the Organ Mts. as viewed from the west. Fig. 2 shows a canyon located toward the southwestern end of the range. This is typical habitat for the new subspecies of *Fixsenia polingi* (Barnes & Benjamin) described below.

Incisalia henrici solatus Cook & Watson, 1909

In March 1979, R. Holland collected a series of *Incisalia* in a canyon on the western side of the Organ Mts. Specimens that he subsequently sent to me for an opinion proved to be *Incisalia henrici*, previously known in New Mexico only from Guadalupe Ridge near Carlsbad. For the present, I have placed this material as *solatus*. It matches well some of my examples from western Texas, and is clearly not the longer-tailed *turneri* Clench. *I. h. solatus* was described from 17 specimens taken in Blanco Co., Texas, and Holland's material fits the original description quite well. Cook and Watson did not illustrate *solatus*. A female from New Mexico is shown in Figs. 3–4.

There are several phenotypes of *henrici* in Texas, and the material from western Texas needs considerable further study. With such study, *henrici* from the Organ Mts. may prove to be a new subspecies, as is the case with *Fixsenia polingi*, described subsequently.

Fixsenia polingi (Barnes & Benjamin), 1926

A preliminary note about hairstreak nomenclature is necessary: in 1961, Harry Clench erected the new genus *Euristrymon* containing the species: *favonius* J. E. Smith, *ontario* W. H. Edwards, and *polingi* Barnes & Benjamin. In a 1978 paper, Clench lumped *Euristrymon* as a synonym of *Fixsenia* Tutt, 1907. *Fixsenia* was originally applied to Old World fauna with the Asiatic type species *Thecla herzi* Fixsen, 1887.

On the morning of 28 May 1979, I was collecting on one side of Texas Canyon (WSMR) in the Organ Mts., when I netted a specimen of *Fixsenia polingi* nectaring at the white flower of a shrub. The collection site included a small oak grove. Several additional specimens were taken that afternoon. Subsequent collecting in other canyons on both sides of the mountain range by R. Holland, B. Harris and the author produced a small series of *polingi*.

As reported for Texas (Davis Mts.), the butterflies were always associated with scrub oak. Several species or varietal forms of scrub oak occur in the Organs, and the butterflies did not seem to be restricted to any one kind. A few specimens were taken on flowers, especially *Asclepias asperula* (Decne.) Woodson, a low-growing milkweed with inconspicuous greenish-white flowers. The majority of the specimens were collected by the time-honored method of beating the oaks. When startled in this manner,

FIG. 1.   Organ Mts. viewed from west.
FIG. 2.   Typical canyon in Organ Mts. where *F. polingi* flies.

the butterflies would generally fly about 100 feet and settle on another scrub oak. Occasionally they would return to their initial perch. Others just disappeared into the haze, thus frustrating the collector. The oaks normally grow on fairly steep talus slopes and collecting *polingi* is not an easy matter. The butterflies are quite wary, especially after being disturbed initially.

Recent examination of the specimens collected indicated several consistent differences between *polingi* from the Organ Mts. and material from the only other known

FIGS. 3–4. *Incisalia henrici solatus*: **3,** ♀ (dorsal), Organ Mts., March 1979, R. Holland collector; **4,** same (ventral).

populations in the Davis Mts. and Big Bend area of Texas. The Davis Mts. butterfly is designated *Fixsenia polingi polingi* (Barnes & Benjamin), and a new subspecies is described for material from the Organ Mts., Doña Ana Co., New Mexico. Texas specimens are shown in Figs. 5–8.
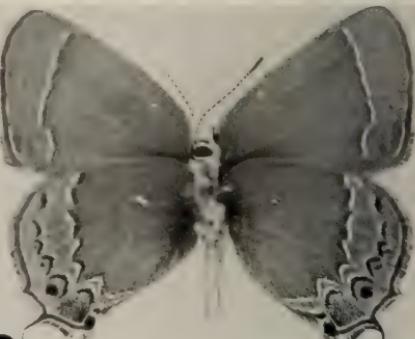
FIGS. 5–8. *Fixsenia polingi polingi*: **5,** ♂ (dorsal), 10 mi N of Alpine, Brewster Co., Texas, 1 June 1973, leg. J. Harry; **6,** same (ventral); **7,** ♀ (dorsal), same data; **8,** same (ventral).
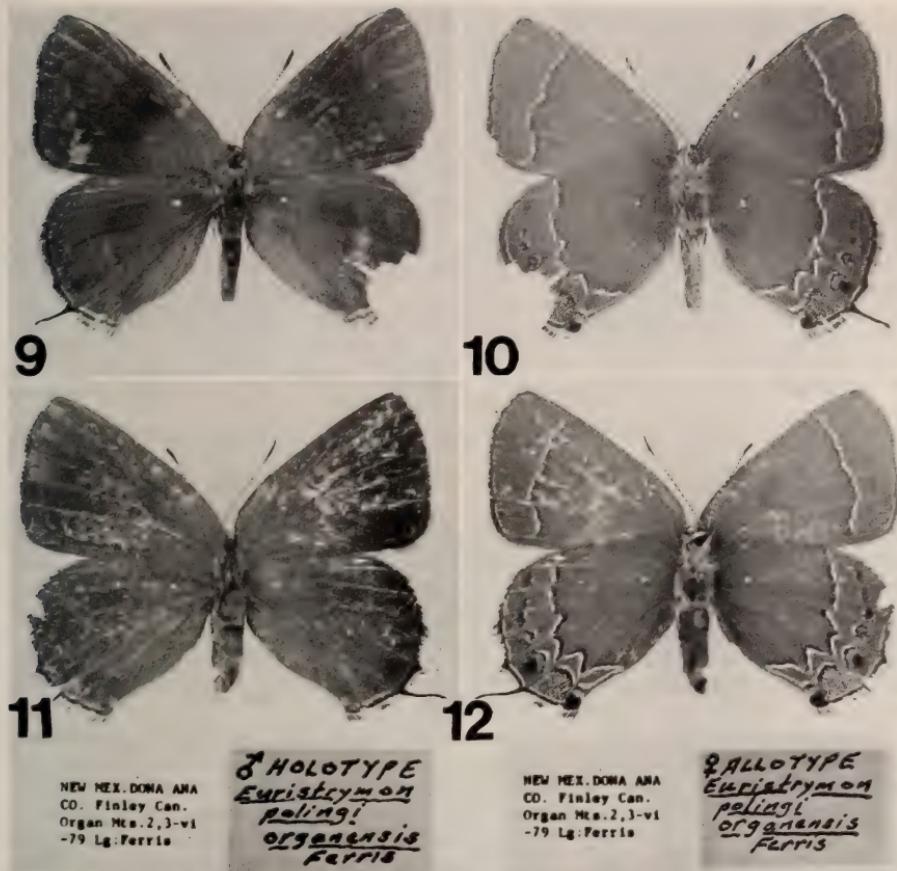
FIGS. 9–12.　*Fixsenia polingi organensis*: **9,** Holotype ♂ (dorsal); **10,** same (ventral); **11,** Allotype ♀ (dorsal); **12,** same (ventral); specimen labels.

Fixsenia polingi organensis Ferris, **new subspecies**

The original description of *Strymon polingi* appeared in a supplement to the general checklist of North American butterflies published by Barnes & Benjamin (1926a, b). The type series consisted of a Holotype ♀ [*sic*, male assumed], Allotype ♀ and 125 Paratypes of both sexes, collected on the Sunny Glen Ranch nr. Alpine, Brewster Co., Texas. The published description is limited to six short sentences in which the new species is compared with various aspects of [*Phaeostrymon alcestis*] *alcestis*, [*P. alcestis*] *oslari*, [*Fixsenia ontario*] *autolycus*, and [*F. ontario*] *ontario*. There is no clear description and *polingi* is not illustrated.

In the following paragraphs, I emphasize the differences between *polingi* and *organensis*. The text description of *polingi* in Howe (1975, p. 301) is incorrect in several respects, although the illustrations (Pl. 52, F. 19–20) are accurate.

Types and location.　This subspecies is described from 15 specimens in the C. D. Ferris collection, collected in the Organ Mts., Doña Ana Co., New Mexico, in late May and early June 1979. The Holotype male and Allotype female were collected in Finley Canyon, W slope Organ Mts., 2, 3 June 1979, ca. 6500 ft (1980 m). They have been
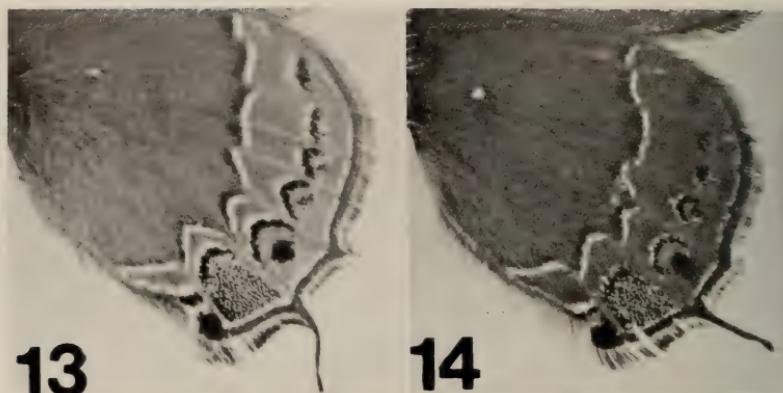
FIGS. 13–14. *Fixsenia polingi*: **13**, *polingi* ♂ VHW; **14**, *organensis* Holotype ♂ VHW.

placed in the Allyn Museum of Entomology, Sarasota, Florida. They are illustrated with their labels in Figs. 9–12. The locality labels are machine-printed black-on-white. The red Holotype and green Allotype lables are hand-printed in black ink. The 13 Paratypes are presently in the author's collection. R. Holland was in Central America when this paper was prepared; consequently his specimens were not available for inclusion in the type series. The Paratypes are as follows: Finley Canyon, 2, 3 June 1979, 3♂, 2♀; Texas Canyon (WSMR), 28 May 1979, 2♂; canyon in central portion of Organ Mts., NW of Texas Canyon, 29 May 1979, 5♂, 1♀.

Diagnosis and description. Except as noted below, the sexes are similar. **Head. Antennae.** Approximately 55% of length of FW costa; ringed black-and-white; tip, yellow-orange. **Palpi.** White with some black hairs (dark hairs more extensive in *polingi*). **Eyes.** Brown, slightly hairy. **Face** (frontoclypeal sclerite). Covered with charcoal-gray hairs (dark brown hairs in *polingi*). **Thorax.** Dorsal color matches dorsal ground color of wings; ventrally covered with white and dark hairs producing an overall charcoal-gray aspect (pale brownish-gray aspect in *polingi*). **Legs.** Femur and tibia colored as in ventral thorax; tarsomeres black-and-white banded. **Abdomen.** Dorsal color matches dorsal ground color of wings; slightly paler ventrally. **Wings.** Ground color dark gray-brown dorsally; slightly paler ventrally. No fulvous (Smithe nos. 16–17) DFW patches in females as frequently seen in *polingi*. DHW subterminal fulvous lunule, frequently found in *polingi*, is either absent or very weakly expressed in *organensis*. The basad white lunule caps are nearly obsolete, while prominent in *polingi*. The aspect presented by *organensis* is that of a single postdiscal band with a weak submarginal spot/lunule row; *polingi* presents more of a double-banded aspect. There is a suggestion of a second HW tail in *polingi*; only a marginal irregularity appears in *organensis*. On the VFW of *polingi*, there is a weakly defined submarginal band of elongated spots, distal to the white linear band; these spots are absent in *organensis*. The FW of both sexes are very similar in shape, and more rounded than in other *Fixsenia* species. **Expanse** (FW costa). Holotype: 16 mm; male range: 15–16.5 mm. Allotype: 16.5 mm; female range: 15–18 mm.

Male genitalia. Genitalia of *polingi* and *organensis* are identical.

Variation. Other than the absence or presence of the DHW orange lunule and the size of the DFW scent pad in the males, there is essentially no pattern variation in the type series.

Etymology. The name is a Latinization of the name of the mountain range in which the type series was collected. There is no word in classical Latin for organ, since this musical instrument was unknown during the Roman Empire.

Bionomics and distribution. Nothing is known of the life history. The adults are always in association with several species or varietal forms of scrub oak. The flight period appears to be the the last week of May and the first week in June. This subspecies seems to be widely distributed throughout the Organ Mts. wherever scrub oak occurs. Many more specimens were seen than the type series indicates. Collecting this insect is not easy because of the habitat terrain; one must also contend with numerous rattlesnakes (at least three species), and many thorned plants.

ACKNOWLEDGMENTS

LITERATURE CITED

BARNES, W. & F. H. BENJAMIN. 1926a. Check list of the diurnal Lepidoptera of boreal America. Bull. So. Calif. Acad. Sci. 25: 3–27.
——— 1926b. Notes on diurnal Lepidoptera, with additions and corrections to the recent "List of diurnal Lepidoptera." Bull. So. Calif. Acad. Sci. 25: 88–98.
COOK, J. H. & F. E. WATSON. 1909. *Incisalia* (Lepidoptera) from Texas. Canad. Ent. 41: 181–182.
CLENCH, H. K. 1978. The names of certain hairstreak genera (Lycaenidae). J. Lepid. Soc. 32: 277–281.
HOWE, W. H., ED. 1975. The Butterflies of North America. Doubleday & Co., Inc., Garden City, New York. 633 pp.
SMITHE, F. B. 1976. Naturalist's color guide. Amer. Mus. Nat. Hist., New York.

Note added in proof: R. Holland took a single specimen of *organensis* in the Capitan Mts., Lincoln Co., New Mexico, in 1980.

A NEW MUTANT OF *DANAUS PLEXIPPUS* SSP.
ERIPPUS (CRAMER)

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ABSTRACT. A mutant form of *Danaus plexippus* f. *erippus*, controlled by an autosomal recessive gene, is described from Argentina. It appears to differ from the "albino" form occurring in Hawaii.

In 1978 Mr. Robert Goodden kindly sent us eggs and larvae of *Danaus plexippus* ssp. *erippus* (Figs. 1–9) derived from Buenos Aires, Argentina. The larvae were easily reared on species of *Asclepias* and the insects (the "main stock") were released in heated greenhouses both on Merseyside and at Ashton in Northamptonshire. In the next generation of insects there appeared in both sexes an unusual aberration, and as far as we know a description of this has not previously been published. In its most extreme form the cell on both the upper and undersides of the forewing is very pale yellowish-cream colored instead of orange. Pale yellow areas are also a feature in the subapical region and there is a thin line of this color along the costal margin of the forewings. In general the abnormality is much more marked in the female (Figs. 5, 6) than in the male (Figs. 7–9). None of the pale yellow areas fluoresced under ultraviolet light.

It seemed possible that this unusual pattern was controlled by an autosomal recessive mutant gene in double dose and our breeding results (Tables 1–3) support this view.

Autosomal Inheritance of the Pattern

The locus controlling the mutant gene cannot be on the nonpairing part of the Y chromosome because mutant females have given rise to mutant males (see Table 1, brood 15619, and all three broods in Table 3).

X-linkage is contradicted by brood 15575 (see Tables 1 and 2) because mutants of both sexes appeared in the offspring of normal parents which must both have been heterozygotes. If the gene had been

TABLE 1. Parents and progeny of broods involving the mutant form of *Danaus plexippus erippus* from Argentina.

	Parents		Offspring				Remarks
			normal		mutant		
	♀	♂	♂♂	♀♀	♂♂	♀♀	
15440	"main stock" mutant	"main stock" normal	4	2	—	—	Consistent with recessive hypothesis
15469	"main stock" mutant	"main stock" normal (same as 15470)	4	5	4	5	Consistent with backcross
15470	"main stock" normal	"main stock" normal (same as 15469)	2	3	1	1	Consistent with mating of two heterozygotes and gives the expected ratio
15473	"main stock" mutant	"main stock" (form unknown)[1]	2	1	3	1	Consistent with backcross
15575	15440 normal	15440 normal	32	15	5	10	Consistent with mating of two heterozygotes and gives the expected ratio
15598	15470 mutant	15470 (form unknown)[1]	4	4	2	3	Consistent with backcross
15601	15470 normal	15470 normal	9	17	5	7	Consistent with mating of two heterozygotes
15619	"main stock" mutant	"main stock" mutant	—	—	4	—	Consistent with recessive hypothesis

[1] Mating not observed.
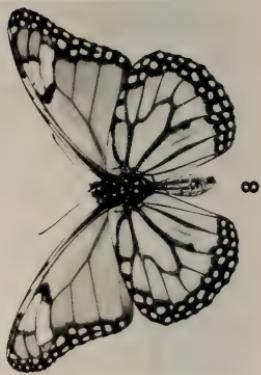
FIG. 10. Male "albino" Hawaiian monarch. Honolulu, ex larva 21 Dec. 1976, F. G. Howarth, collector. Photograph courtesy of the Dept. of Photography, B. P. Bishop Museum, Honolulu, Hawaii, L. Gilliland & J. C. E. Riotte.

X-linked the mother would have been of the mutant form. We can therefore safely say that the mutant gene is autosomal.

FERTILITY

We had no difficulty in breeding from the heterozygous stock but our impression is that the mutant butterflies are relatively inactive and that the mutant × mutant mating is very infertile. Thus from two mutant males and three mutant females put together in a separate greenhouse we only obtained eggs from one female and many of these were infertile. Only four mutant males resulted (brood 15619, Table 1).

←

FIGS. 1–9. Normal and mutant phenotypes of *Danaus plexippus* ssp. *erippus* from Argentina stock. **1–2,** normal male; **3–4,** normal female; **5–6,** mutant female; **7–8,** mutant male; **9,** less extreme mutant male. First photo = dorsal view; second photo = ventral view of each specimen.

TABLE 2. Totals of matings between presumed heterozygotes.

		Offspring			
		Normal		Mutant	
	Parents	♂♂	♀♀	♂♂	♀♀
15470	normal ♀ × normal ♂	2	3	1	1
15575	normal ♀ × normal ♂	33	15	5	10
15601	normal ♀ × normal ♂	9	17	5	7
		44	35	11	18

COMMENT

Mutations arise by chance and are usually deleterious because they upset the adjustment of the organism to its environment. However, sometimes they may be advantageous and this needs particular consideration in the case of models and mimics. For example, if mimics of any given model become too common, the models escape by evolving new patterns (as is probably the case in *Danaus chrysippus*). This series of events is unlikely to occur in the case of *erippus* since it is not only a poor storer of cardenolides (though a good sequesterer of pyrrolizidine alkaloids, which are probably equally important for defense purposes (Rothschild & Marsh, 1978)) but its mimics are conspicuous by their absence. The only possible contender is *D. gilippus xanthippus*, but the flight periods of the two butterflies in Brazil barely overlap—except briefly in October and February. Since both species feed as larvae and adults on the same plants (Biezanko, 1960) they may possibly present a case of "tandem" mimicry (Rothschild, 1963). However in Hawaii, where *Danaus plexippus* is the only *Danaus* recorded (Zimmerman, 1958), a white form, Fig. 10, occurs at a frequency up to 4% (R. Silberglied in litt. via the Bishop Museum) but it does not closely resemble the mutant described here. The circumstances which favor this high survival rate are certainly worth investigation.

TABLE 3. Totals of presumed backcrosses.

		Offspring			
		Normal		Mutant	
	Parents	♂♂	♀♀	♂♂	♀♀
15469	mutant ♀ × normal ♂	4	5	4	5
15473	mutant ♀ × normal ♂	2	1	3	1
15598	mutant ♀ × normal ♂	4	4	2	3
		10	10	9	9

LITERATURE CITED

BIEZANKO, C. M. 1960. Danaidae et Ithomiidae da zona sueste do Rio Grande do Sul (Contribução ao conhecimento da fisiografica do Rio Grande do Sul). Arq. Entomol. Pelotas (A) 3: 1–6.

ROTHSCHILD, M. 1963. Is the Buff Ermine (*Spilosoma lutea (Hufn.)*) a mimic of the White Ermine (*Spilosoma lubricipeda (L.)*)? Proc. Royal Entomol. Soc., London, ser. A., 38, parts 7–9, pp. 159–164.

ROTHSCHILD, M. & MARSH, N. 1978. Some peculiar aspects of Danaid/plant relationships. Entomol. Exp. and Appl. 24, pp. 437–450.

ZIMMERMAN, E. C. 1958. Insects of Hawaii, Vol. 7 (Macrolepidoptera) Univ. Hawaii Press xiv + 542 p. 423 figs.

A NEW HIGH ALTITUDE SPECIES OF *BOLORIA* FROM SOUTHWESTERN COLORADO (NYMPHALIDAE), WITH A DISCUSSION OF PHENETICS AND HIERARCHICAL DECISIONS

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ABSTRACT. A new *Boloria* was collected for the first time in July 1978 on Mt. Uncompahgre in southwestern Colorado. It is described as a full species, *B. acrocnema*, most closely related to *B. improba* whose southern limit is more than 1800 km to the north. Adult characters, including genitalia, wing-pattern and venation, and ultraviolet reflectance patterns, are analyzed numerically. Classical and numerical taxonomic approaches to this situation are contrasted, and the utility of phenetics in hierarchical decisions is discussed. A practical guide to specimen recognition, and some aspects of the distribution and ecology of the butterfly are also presented.

Butterfly systematists lately have recognized a number of phenotypically cryptic species after closer examination of already amassed material (e.g., Stallings & Turner, 1954; Burns, 1960; Remington, 1968; Cardé, Shapiro, & Clench, 1970; Clench, 1972), and it is likely that many more distinct species remain undetected in the major collections. New and previously uncollected butterfly species, in contrast, are rarely being discovered in temperate North America. *Sandia macfarlandi* (Ehrlich & Clench, 1960) is the most prominent recent discovery of this kind.

On 30 July 1978 a party of five from the Rocky Mountain Biological Laboratory (including Scott M. Graham, Kathleen A. Shaw, Wendy E. Roberts, and the authors) discovered a colony of a hitherto unknown *Boloria* some 600 to 700 m above timberline on Mt. Uncompahgre, Hinsdale County, Colorado. In general appearance the Uncompahgre specimens are most similar to specimens of the circumpolar butterfly *B. improba* (Butler), but they possess an array of different phenotypic characteristics. We have concluded that this taxon represents a distinct species, for reasons discussed in detail below, and it is described as new, as follows.

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Boloria (Clossiana) acrocnema Gall & Sperling, **new species**

Description. **Male** (Figs. 1–6). **Head:** eyes dark brownish black; clypeal and vertex hairs rust brown; mean length of antenna 7.8 mm (range = 7.4–8.4; holotype 7.9. This format is followed throughout species description; sample numbers as in Characteristics section), shaft light brownish black, checkered with white, club black with orange terminus; labial palps clothed with black and rust brown hairs. **Thorax:** clothed dorsally with rust brown hairs, white hairs interspersed posteriorly; femora covered with long rust brown hairs, tibiae and tarsi with shorter light brown hairs. **Abdomen:** deep brownish black, clothed with long rust brown hairs; segments VII–VIII with numerous white hairs ventrally. **Forewing:** mean length 15.8 mm (14.9–17.1; 15.4), width 8.0 mm (7.5–8.5; 7.8); margins distinctly rounded. Dorsal surface: ground color golden brown, variably flushed with white basad of postmedian band; heavy melanization confined to basal area, long white hairs covering this region; outer margin checkered black and white; postmedial, medial, and subbasal bands black, thin, and contrasting sharply with ground color; postmedial band in cells M_3 and Cu_1 closely adjoining discocellular crossvins; veins R_2 to R_4 branching from radial stem near apex; submarginal band extending to inner margin through cell Cu_2, with a prominent cross bar connecting with postmedial band; rounded spot present in variable position in postbasal section of discal cell; submarginal spots large and oblong, filling one-fourth to one-half of cells, the most caudad spot filling greater than or equal to one-half of its cell and joined to marginal band. Ventral surface: ground color light golden brown, flushed marginally with reddish brown; veins and bands brownish black to black, contrasting with ground color. **Hindwing:** mean length 12.0 mm (11.4–12.5; 11.5), width 8.9 mm (8.2–9.8; 9.0), margins distinctly rounded. Dorsal surface: ground color golden brown, often flushed with white in discal area; heavy melanization confined to basal area and anal margin below disc; outer margins checkered black and white; conspicuous D-shaped whitish or golden patch in basal section of discal cell; maculation black, contrasting with ground color. Ventral surface: discal ground color deep cinnamon-brown, contrasting with golden brown limbal area; submedian-median row complete, heavily flushed with silvery-white, indented sharply at junction of discal cell and cells Cu_1/Cu_2; submedian-median row thin below discal cell, directed toward anal angle; several white basal spots present. **Male genitalia:** uncus horn-shaped, mean length 0.40 mm (0.38–0.43; 0.40), lateral processes diverging perpendicularly; caudal section of tegumen heavily sclerotized, diverging cephalad slightly from the center; inner face of valve covered with numerous small setae, mean length of valve 1.63 mm (1.56–1.68; 1.62); cucullus stout, covered with long setae, a single thick prong projecting inward at terminus; digitus slender, mean length 0.43 mm (0.38–0.47; 0.46), distal end slightly distended and covered with small spines; juxta U-shaped, dorsal projections bilobed; mean length of aedeagus 1.42 mm (1.37–1.55; 1.52), distal half slender with a single long rostellum, proximal half slightly distended; caecum short and blunt.

Female (Figs. 7–12). **Head:** as in male, but palps browner; mean length of antenna 8.2 mm (7.7–8.6; allotype 8.0). **Thorax:** as in male. **Abdomen:** as in male, but with white hairs confined to immediate area of genital opening. **Forewing:** maculation patterns and coloration as in male with the following exceptions: connecting bar in cell Cu_1 variably expressed, submarginal spots extending over smaller area in their cells, the most caudad spot occasionally joined to marginal band. **Hindwing:** as in male. **Female genitalia:** lamella postvaginalis a finely sculptured funnel, open and membranous at distal end; lamella antevaginalis with wide semicircular lobes projecting ventrad; posterior section of genital plate forming two semicircular plates articulating laterally, their ventral margins covered with soft hairs; papillis analis soft, sparsely covered with short hairs, apophysis posterioris short; sternum VII forming thin rectangular plate over lamellae and ductus bursae; entire genitalia lightly sclerotized.

Type series. All specimens of B. acrocnema captured in 1978 have been designated as primary types or paratypes. Locality data for each is as follows: taken 30 July 1978 on Mt. Uncompahgre, 13.0 km NW of Lake City, Hinsdale Co., Colorado, elev. 4080–4140 m. The Holotype ♂, Allotype ♀, and 18 paratypes (12 ♂, 6 ♀) have been placed
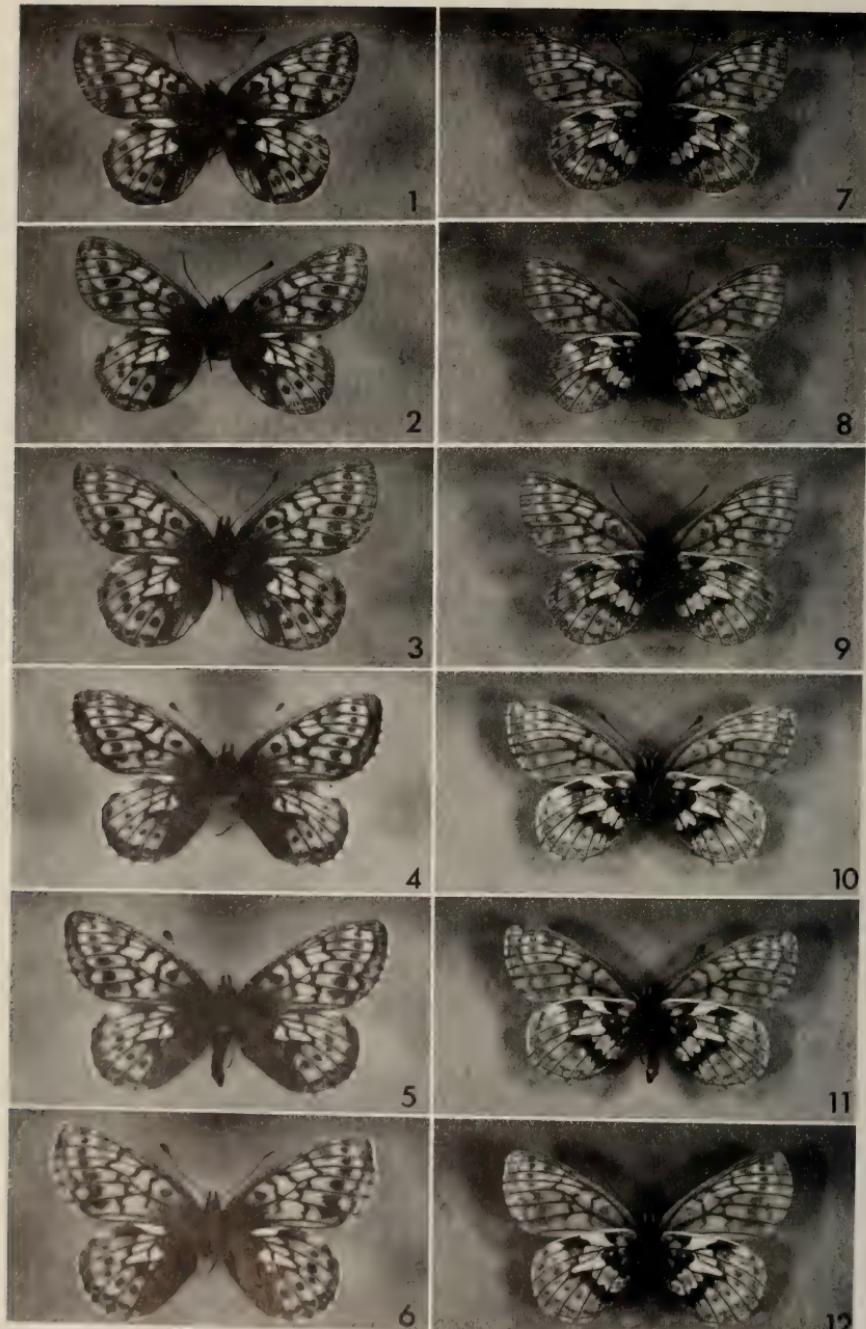
FIGS. 1–12. Specimens of *Boloria acrocnema*, new species. Figs. **1–6.** Dorsal surfaces: **1–3**, males (1, Holotype); **4–6**, females (4, Allotype). Figs. **7–12.** Undersurfaces of same specimens in Figs. 1–6. All specimens taken 30 July 1978, Mt. Uncompahgre, Hinsdale Co., Colorado, elev. 4080—4140 m, leg. L. F. Gall & F. A. H. Sperling.

TABLE 1. Characters most readily used when separating specimens of *B. acrocnema* and *B. improba*. Full descriptions of the characters are given in the text. See also Figures 13–24.

Character	*B. acrocnema*	*B. improba*
1. FW radial veins R_2–R_4	branching near apex	branching further down radial stem
2. Dorsal melanization	confined basally	extensive
3. Overall maculation	thin; contrasting with ground coloration	wide; blurred
4. Postmedial DFW band	offset; close to crossveins in M_3 and Cu_1	more connected; further margined
5. DHW discal cell spot	clear, crisp	obscured
6. VHW submedian-median row	complete; silvery-white; strongly indented basally	absent to complete, duller yellow; not indented
7. Uncus and tegumen processes	T-shaped	Y-shaped
8. Valve length	1.54–1.66 mm (mean = 1.63 mm)	1.78–2.06 mm (mean = 1.92 mm)

in the Peabody Museum of Natural History, Yale University. Three paratypes (2 ♂, ♀) have been placed in the Canadian National Collection, Ottawa, four (2 ♂, 2 ♀) in the American Museum of Natural History, New York, and another 14 (8 ♂, 6 ♀) have been retained in the personal collections of Kathleen A. Shaw and the junior author. Total number in type series 41 (25 ♂, 16 ♀).

Etymology. The name is a latinization of the Greek roots *acro* (the top of) and *cnemus* (the mountain slope), descriptive of the type locality. The adjectival specific name, which conforms in gender to the feminine *Boloria*, may be pronounced either ă-krō-NĒ-ma or ă-krō-KNĒ-ma. We suggest the Uncompahgre Fritillary as a common name.

Remarks. Characteristics of *B. acrocnema* **compared to those of** *B. improba*. The most useful characters distinguishing *B. acrocnema* from other *Boloria*, especially *B. improba*, are described below and in Table 1, and are shown in Figs. 13–24. 117 specimens have been examined for wing-pattern and venation characteristics: 20 ♂, 11 ♀ *B. acrocnema*; 15 ♂, 21 ♀ *B. i. improba* (Butler); 19 ♂, 17 ♀ *B. i. youngi* (Holland); 9 ♂, 5 ♀ *B. i. improbula* (Bryk): for male genitalia: 10, 6, 16, and 4, respectively. We hereafter use specific localities, and the general geographic terms North American arctic, Canadian subarctic (=western Hudsonian and northeastern Montanian biotic provinces of Dice, 1943; see also Freeman, 1956), and Scandinavian arctic, respectively, in reference to the *B. improba* populations analyzed. Unless otherwise indicated, *B. improba* refers to the specimens from all geographic areas. Metric data are arithmetic means in millimeters; most were taken from the phenetic analyses.[2]

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[2] Differences in character distributions between *B. acrocnema* and, in each case, the most similar geographic sample of *B. improba* are all significant at the 0.05 level (all but two at the 0.01 level, these distributions being essentially non-overlapping in range). Those among the *B. improba* samples, except the ratio of digitus length to valve length (roughly, North American arctic > Canadian subarctic = Scandinavian arctic at the 0.05 level) are insignificant (p > 0.10; Mann-Whitney U-tests, degrees of freedom vary according to sample comparisons). Metric data for Albertan specimens of *B. improba* have been lumped with those from other Canadian subarctic localities for analysis (due to small sample size: 3 ♂, 3 ♀), although this population has been discussed separately on occasion in the text. Female Scandinavian arctic *B. improba* have not been numerically analyzed either due to small sample size. Statistical methods follow Sokal & Rohlf (1969) and Rohlf & Sokal (1969).

Table 1 gives a synopsis of those characters we find most expedient when sorting pinned specimens. These and other differences are discussed in greater detail here. The dorsal maculation patterns in *B. acrocnema* are sharp, contrasting with the ground coloration (cf. normally very blurred in *B. improba*), and the vertical dashes comprising the medial and postmedial forewing bands are thinner and less colinear than in *B. improba*. The postmedian forewing band in cells M_3 and Cu_1 is located much closer to the discocellular crossveins in *B. acrocnema*. The submedial forewing band extends directly through cell Cu_2 to the outer margin, usually with a thick bar extending distad to the postmedian band; the former character is located further basad in *B. improba*, the distance between the bands being greater (most visible on ventral forewing surface). Specimens of *B. acrocnema* exhibit a prominent, free-standing basal forewing spot, whereas in virtually all *B. improba* this same spot is squarer and broadly connected to the costal and cubital stem. The most caudad spot of the forewing submarginal band is large and broadly connected to the marginal band in *B. acrocnema*, but is smaller and free-standing in *B. improba*. Heavy melanization extends across much of the forewing basal area and 50–75% of the hindwing in *B. improba*, especially in material from the District of Franklin, Canada, but is quite restricted in *B. acrocnema*. The D-shaped patch in the basal section of the hindwing discal cell is crisply delimited in *B. acrocnema*, but obscured in *B. improba* (sometimes totally absent in North American arctic material).

The forewing veins R_4, R_3, and especially R_2 are all shorter in *B. acrocnema* (males: 2.98, 4.04, 5.15; females: 3.28, 4.38, 5.68) than in North American arctic (3.42, 4.97, 6.41; 3.76, 5.52, 7.03), Canadian subarctic (3.58, 5.12, 6.68; 3.85, 5.56, 7.23), and Scandinavian arctic (3.67, 5.23, 6.43) *B. improba*. These veins thereby appear compressed near the apex in *B. acrocnema*. The white circles in Figs. 13–18 indicate their branch points from the radial stem. In addition, the length-to-width ratios of fore- and hindwings of *B. acrocnema* (1.97, 1.31; 1.96, 1.29) are slightly greater than in North American arctic (1.89, 1.19; 1.88, 1.21), Canadian subarctic (1.87, 1.21; 1.87, 1.21), and Scandinavian arctic (1.88, 1.22) *B. improba*. The marginal wing angles are also distinctly rounded in *B. acrocnema*, and when coupled with the ratio characters, they give its wings an oblong appearance.

Ventrally in *B. acrocnema* the well-defined submedian-median row is complete, heavily flushed with silvery-white, and contrasts strongly with the surrounding ground coloration (deep cinnamon-brown). This row is incomplete in North American arctic *B. improba* (often entirely absent in material from the Northwest Territories of Canada) and more complete in Canadian subarctic material, but is wider, duller yellow, and less contrasting with the ground coloration (yellow- to orange-brown). In Scandinavian arctic *B. improba* the row is sometimes complete, but is not as contrasting or heavily flushed with silvery-white. In *B. acrocnema* this row is also conspicuously indented basally near the junction of cells Cu_1/Cu_2 and the discal cell, and is directed toward the anal angle. In *B. improba* the band is not indented and is directed more toward the inner margin. The most cephalad spot of the submedian-median row (white costal

→

FIGS. 19–24.   Representative genitalic differences between *Boloria acrocnema* and *Boloria improba*. Figs. **19–21.** Paratype of *B. acrocnema*: **19,** ventral view showing width of saccus; **20,** cephalic view showing length of uncus and shape of uncal/tegumen processes; **21,** lateral view showing length of valve, and associated structures. Figs. **22–24.** Same characters from a specimen of *B. i. youngi*, figured as representative for the species. Locality data as before. Each pair of photographs taken at the same magnification; scale bars are 0.25 mm.

spot) is thin and strongly concave basally in virtually all *B. improba* but is wider and straight in *B. acrocnema*.

In the male genitalia of *B. acrocnema* the more heavily sclerotized caudal sections of the tegumen diverge cephalad from the center only slightly, as do the lateral processes of the uncus, the combination appearing T-shaped when viewed dorsally (Fig. 20). These same structures diverge considerably and appear Y-shaped in *B. improba* (Fig. 23). The uncus length, valve length, and saccus width are all smaller in *B. acrocnema* (0.40, 1.63, 0.79) than in North American arctic (0.47, 1.92, 0.98), Canadian subarctic (0.50, 1.94, 1.10), and Scandinavian arctic (0.47, 1.90, 0.98) *B. improba* (see Figs. 19–24). Indeed, the entire genitalia of *B. acrocnema* are noticeably smaller than in *B. improba*. There are also a number of differences in proportion; for example, the ratio of digitus length to valve length is greater in *B. acrocnema* (0.27) than in North American arctic (0.23), Scandinavian arctic (0.21), Albertan (0.18), and other Canadian subarctic (0.21) *B. improba*.

Although generally similar to the visible facies pattern, the ultraviolet reflectance pattern of the ventral surface of *B. acrocnema* highlights the prominent submedian-median row, which is absent or present only as a trace in Nearctic *B. improba* (Figs. 25–27; characters most noticeable in males). Only the lower half of the discal cell spot appears strongly reflective in *B. improba* (cf. entire cell in *B. acrocnema*).

The foregoing classical taxonomic comparisons indicate our butterfly is distinct, and this leads to the next question: at what hierarchical position should *B. acrocnema* be placed? Only *B. acrocnema* and its phenotypic nearest neighbor, *B. improba*, are treated in detail above.

FIGS. 25–27. Ventral surface ultraviolet reflectance patterns of *Boloria acrocnema* and *Boloria improba*. **25,** *B. acrocnema*; **26,** *B. i. youngi*; **27,** *B. i. improba*. Males in upper row, females in lower row of each figure. Taken with PAN-X film and standard Wratten filter. Characters discussed in text.

Although customary when new taxa are erected, such one-to-one morphometric comparisons often do not adequately address questions of rank (e.g., species or very distinct subspecies?). The present situation involves phenotypically discrete populations in extreme allopatry, which of course prohibits analysis of sympatric interactions, the most useful test of biological distinctness. Hybridization experiments have not yet been undertaken to measure genetic incompatibilities, and biochemical data are also unavailable. Moreover, the general life his-

tories and ecologies of *B. acrocnema* and *B. improba* are not yet well known. Another method for indexing rank is to compare their phenotypic distinctness with other similar *Boloria*. An argument may be constructed as follows: if the degree of overall phenotypic difference between *B. acrocnema* and *B. improba* is comparable to that between universally accepted, closely related species, then *B. acrocnema* should also be treated as a distinct species. Since *B. frigga* (Thunberg), *B. bellona* (Fabr.), and *B. epithore* (Edw.) are phenotypically close to *B. improba*, and these four species have been associated as members of the subgenus *Clossiana* (e.g., Warren, 1944; dos Passos & Grey, 1945; Klots, 1951; dos Passos, 1964; Higgins & Riley, 1970), we thus use them here for comparison. In addition, analyzing intraspecific variation within each *Boloria* species (e.g., Perkins & Meyer, 1973 for *B. epithore*) provides the necessary further checkpoints for correlating relative phenotypic differences with differing levels of accepted taxonomic affinity.

Phenotypic variability within and between populations can be great in *Boloria*, and this is especially noticeable in series of *B. improba*. While single- and few-character schemes are sometimes useful in taxonomic inquiry, these methods normally are unable to cope with extensive variability (e.g., Lafontaine, 1970; see Gall, 1976) and cannot give reliable estimates of overall similarity. Accordingly we are employing some of the multivariate techniques of numerical taxonomy in the following investigation.

TAXONOMIC RANK: PHENETIC METHODS

We present a brief overview of our objectives and methods in this work. The next few paragraphs are a partial, non-technical summary of both. Numerical taxonomy encompasses diverse techniques for exploring phenotypic and phyletic relationships. The field grew rapidly with the advent of digital computers in the 1960's, and several subdisciplines have since emerged, most notably cladistics and phenetics. We present some of the techniques and philosophy of the latter.

The methods of phenetics are shared by several fields, including systematics, psychology, economics, and ecology. Systematists have typically employed phenetics or phenetic-like methods for large revisionary works or for inferring phyletic patterns among many taxa, although cladistics are now more frequently used for phyletic interpretation. We are not embarked upon such a broad study; rather, we are using phenetics as a tool for attacking a locally defined problem. Roughly, when using phenetics in taxonomy, one attempts to order taxa into groups defined by quantitative measures of similarity or difference. Sneath & Sokal's (1973) book, Numerical Taxonomy, is the

basic reference treating numerical taxonomic (esp. phenetic) theory and practice. For other approaches to systematic problems, reviews of species concepts, and bases upon which to establish classifications see: Mayr, 1963, 1974; Hennig, 1966; Michener, 1970; Sokal, 1975; Brothers, 1975; and the journal Systematic Zoology.

In numerical taxonomic work one uses many characters simultaneously (anywhere from a few dozen to several hundred). Corollary considerations—among them the effect of character correlation upon the taxonomic pattern—have been posed for techniques such as factor, canonical, and discriminant analysis. We use a kind of factor analysis called principal component analysis, in part since it expedites examination of character correlation and variation in large data sets, and because the method will also faithfully represent phenetic differences among fairly distinct groups (the species and subspecies under comparison; see Rohlf, 1968). For a full discussion of factor analysis and related techniques see Harman (1976). These numerical methods are typically used for detailed descriptions of character-character relationships in large data sets. As an example of another use for principal component analysis, especially for practicing systematists, we screened for various taxonomically discriminating character sets with reference to statistics the computer printed for us (match the relative character weightings given in the Appendix with the positions of the *Boloria* on each principal axis in Fig. 31). Many of the individually diagnostic *acrocnema-improba* characters, and character suites, were first recognized in this manner; a later close inspection of the *Boloria* yielded others.

Before considering the phenetic data, we emphasize two related systematic concerns. Although an old and attractive concept, the possibility of specifying locally (e.g., within *Boloria*) or more globally (e.g., all insect orders) defined standards for measuring hierarchic rank has received relatively little critical attention. Understandably, the necessary prerequisites for such endeavors are synthetic reconciliations of varied species concepts and systematic philosophies. Nevertheless, for many sections of the butterflies, where "splitting" and "lumping" are often practiced simultaneously by different authors, more standardized quantitative approaches (however defined for the present) seem particularly valuable to us. Secondly, classifications and systematic decisions arrived at via phenetic, cladistic, and classical taxonomic techniques tend to converge, especially at lower taxonomic levels. This convergence follows because classical taxonomists have long performed a sort of numerical taxonomy in their heads, perhaps best termed pattern recognition in the broad sense. The convergence holds only to a certain extent. Some groups consis-

tently defy adequate taxonomic structuring *sensu lato* (in the Lepidoptera: *Euphydryas, Colias*, the eastern North American *Hemileuca maia* complex, the *Catocala* [although species boundaries do not seem as much at issue here], and many lycaenid groups, to name a few), and for these phenetic and cladistic treatment would probably be most illuminating.

Materials and Methods

From larger series of available male *Boloria*, 4 *B. i. improba*, 6 *B. i. youngi*, 3 *B. i. improbula*, 3 *B. frigga saga* (Staud.), 2 *B. f. sagata* (Barnes & Benj.), 7 *B. bellona bellona*, 2 *B. epithore epithore* (Edw.), 3 *B. e. chermocki* Perkins & Perkins, 3 *B. e. borealis* Perkins, and 7 *B. acrocnema* were selected for comparative analysis. The genitalia of each were dissected and these individuals scored over an array of 30 genitalic and 45 wing-pattern characteristics. The female analysis involved 4 *B. i. improba*, 4 *B. i. youngi*, 2 *B. i. improbula*, 3 *B. frigga saga*, 3 *B. f. sagata*, 8 *B. bellona bellona*, 2 *B. epithore epithore*, 3 *B. e. chermocki*, 2 *B. e. borealis,* and 6 *B. acrocnema* scored for 39 wing-pattern characteristics. Some wing-pattern characters were easily scored by eye; others and the genitalic characters were scored using a binocular dissecting microscope with an ocular micrometer. The characters employed are listed in the Appendix. Included in the genitalic analysis with *B. i. youngi* were specimens from Prospect Mountain, Alberta, the southernmost population of this butterfly presently known (Pike, 1978).

Specimens of *B. i. youngi* and *B. i. improbula* were borrowed from the American Museum of Natural History. Additional *B. i. youngi* were drawn from the personal collections of G. J. Hilchie, E. M. Pike, and the junior author. Uncompahgre material was drawn from both authors' collections, and all others from the entomological collections at the Peabody Museum of Natural History, Yale University. Locality data for the sample specimens other than *B. acrocnema* are as follows: *B. i. improba*: Chandler Lake and vicinity, and Umiat, Alaska; Baker Lake and Chesterfield, Northwest Territories. *B. i. youngi*: Pink Mountain and Atlin, British Columbia; nr. International border on Alaska Highway, Yukon Territory; Prospect Mountain, Alberta. *B. i. improbula*: Abisko and vicinity, Sweden. *B. frigga saga*: Spray Lake region, Alberta; Riding Mountain, Manitoba. *B. f. sagata*: Gothic and vicinity, Colorado. *B. bellona bellona*: New Haven, Fairfield, and Litchfield Counties, Connecticut; nr. Somerset, Colorado; Burlington and vicinity, Indiana. *B. epithore epithore*: Santa Cruz Mtns., California. *B. e. chermocki*: Salmon Meadows, Okanogan County, Washington. *B. e. borealis*: Mission Mtns., Montana.

At higher taxonomic levels or when highly discrete characters are most plentiful, an "exemplar" approach in numerical taxonomic studies is often feasible (one individual chosen as representative of a taxon, usually species; see Ehrlich & Ehrlich [1967] for an exemplar treatment of world-wide butterfly relationships). Since our taxa exhibit moderate phenotypic variability, we have chosen a level intermediate between the exemplar approach and exhaustive, and costly, analysis of many individuals. Sections of Parks' (1970) FORTRAN IV numerical taxonomy program and others written by the senior author were combined and modified for use on the Yale University Computer Center IBM System/370 computer. This composite program performs the following operations: a) normalization of input character vectors; b) principal component analysis of character variation; c) transformation of original characters to normalized component scores for each specimen; d) construction of a similarity matrix using these component scores and the simple Euclidean distance function (Parks, 1968); e) unweighted pair-group cluster analysis of specimens, again using the distance function. The program then prints a branching tree of phenetic distances (phenogram) in addition to intermediate principal component and cluster analysis parameters. Other options exist, but were not used here. All runs utilized a series of preset default control values during principal components extraction (e.g., minimum of five axes extracted; see Parks, 1970). Varying these conditions (notably, the extraction of additional axes—up to eight in one case) did not alter the basic taxonomic decisions presented below.

Results of Phenetic Analyses

Phenograms of the male genitalic, male wing-pattern, and female wing-pattern relationships were redrawn from the computer output and are shown in Figs. 28–30, respectively. Clusters of *Boloria* separated by more than 35–40% of the maximum distance encountered have been double-spaced for emphasis. A phenogram conveys one-dimensional information; in this case only the horizontal distances have meaning (i.e., all cluster pairs are rotationally symmetric about their higher [right-hand] stems). Distances between specimens are calculated from the origin to the vertical bar connecting them.

In each analysis *B. acrocnema* is readily separable from the others and is phenetically closest to *B. improba*. All described *Boloria* species are readily distinguishable by both wing-pattern and genitalia. Intraspecific variation is diverse, and most ill-defined in *B. improba*. The recognized subspecies of *B. improba* show only weak tendencies to separate on genitalia or wing-pattern characters. Using classical taxonomic methods, Brunn & von Schantz (1948) had pre-

28

29

30
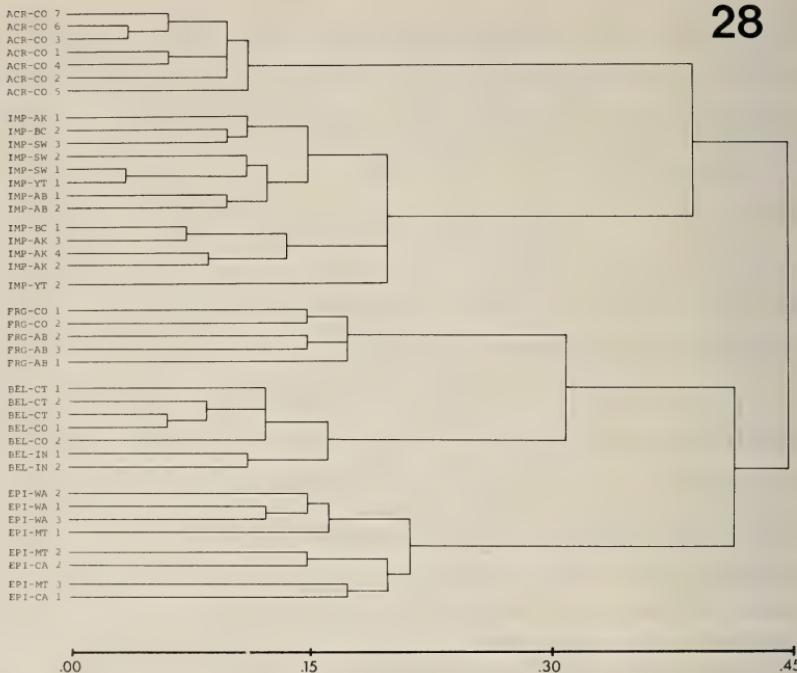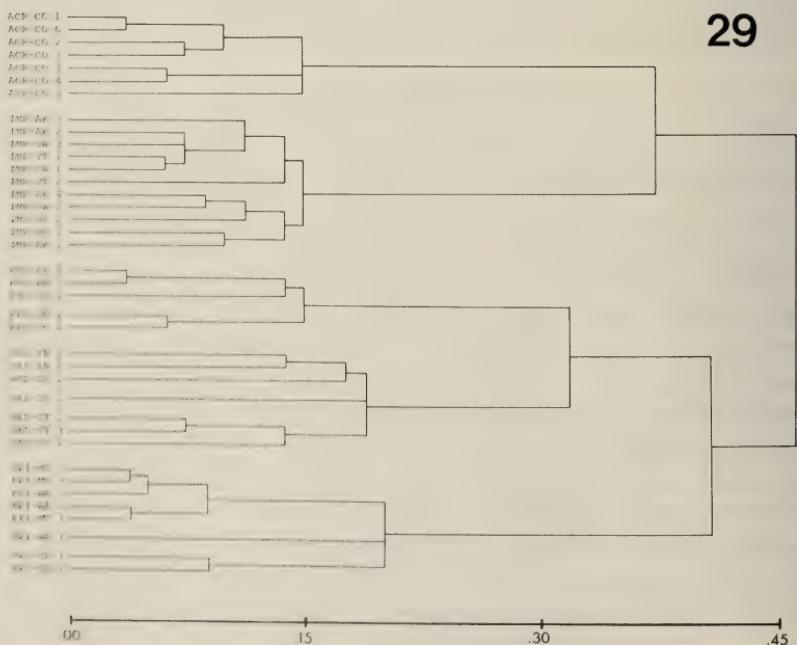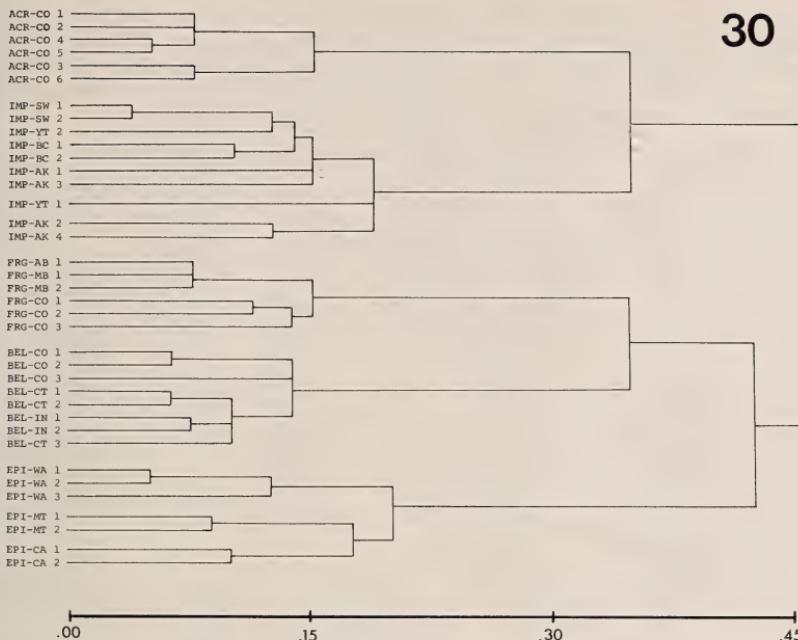
FIGS. 28–30. Phenograms of *Boloria* relationships. **28,** male genitalic phenogram, cophenetic correlation coefficient CPCC = 0.851; **29,** male wing-pattern phenogram, CPCC = 0.877; **30,** female wing-pattern phenogram, CPCC = 0.830. Individuals designated by a three letter acronym, an individual sample number, and a two letter geographic identifier (AB = Alberta; AK = northern Alaska and Northwest Territories; BC = British Columbia; CA = California; CO = Colorado; CT = Connecticut; IN = Indiana; MB = Manitoba; MT = Montana; SW = Sweden; WA = Washington; YT = Yukon Territory). Value of Euclidean distance coefficient, d, given below each phenogram. Note the position change of individual males within, but not between, major clusters in the genitalic and wing-pattern phenograms.

viously found no "constant difference" between the genitalia of Scandinavian and northern Alaskan *B. improba.* The two subspecies of *B. frigga* are readily separable; those of *B. epithore* show variable relationships, with the highly disjunct *B. e. epithore* from coastal California most consistently separated from the others. The widely separated populations of *B. bellona* (not recognized at the subspecific level) are roughly distinguishable, most distinctively on wing-pattern characters.

Phenograms have the advantage of representing multi-dimensional relationships in a single dimension but are consequently subject to problems of distortion. This distortion becomes most apparent at higher level cluster distances, and in many instances can be a serious stumbling block to phyletic extrapolations. Listed in Table 2 are all

Table 2. Pairwise interspecific phenetic distances (d) just prior to final clustering. All individual specimens from within classically defined species have since joined. There are 10 possible species-species distances, and 10 possible intraspecific distances. Three intraspecific distances are for widely separated populations of *B. bellona bellona* not formally recognized at the subspecific level.

	Character set					
	♂ Genitalia		♂ Wing-pattern		♀ Wing-pattern	
Species pair	d	rank d	d	rank d	d	rank d
frigga-bellona	0.310	1	0.317	1	0.349	2
frigga-epithore	0.488	8	0.429	4	0.476	8
frigga-acrocnema	0.524	9	0.506	10	0.463	7
frigga-improba	0.464	7	0.432	5	0.447	6
bellona-epithore	0.362	2	0.392	3	0.393	4
bellona-acrocnema	0.556	10	0.465	8	0.401	5
bellona-improba	0.379	3	0.483	9	0.491	9
epithore-acrocnema	0.452	6	0.459	7	0.527	10
epithore-improba	0.396	5	0.439	6	0.386	3
acrocnema-improba	***0.388***	***4***	***0.372***	***2***	***0.344***	***1***
maximum intraspecific cluster distance	0.201		0.185		0.204	

the possible pairwise species-species phenetic distances, after intraspecific but prior to interspecific clustering (a sort of null hypothesis has been confirmed here: all specimens from within classically defined species have clustered most closely). Reference to the phenograms will indicate the compromises involved during clustering, although in general the unweighted pair-group method tends to conserve phenetic distances i.e., there is no systemic dilation or contraction. Note that the male genitalic and wing-pattern relationships are extremely close, on character suites often considered somewhat divergent in biological process and taxonomic utility.

In order to circumvent the distortion inherent in phenograms, an ordination plot was constructed using the combined sets of male genitalic and wing-pattern characteristics, with the first three principal components extracted as axes (Fig. 31). All 75 characters were used; the Appendix lists the principal component to which each character contributes most heavily. The ordination plot more graphically portrays the distinctness of *B. acrocnema* and the relationships among the various *Boloria*. Since a) *B. acrocnema* is readily distinguishable from its phenotypic nearest neighbor, *B. improba*, b) the phenetic distances between them are comparable to all other species-species distances, and greater than some, and c) these distances are much greater than all intraspecific linkages, we have accorded our Uncompahgre *Boloria* full species status.
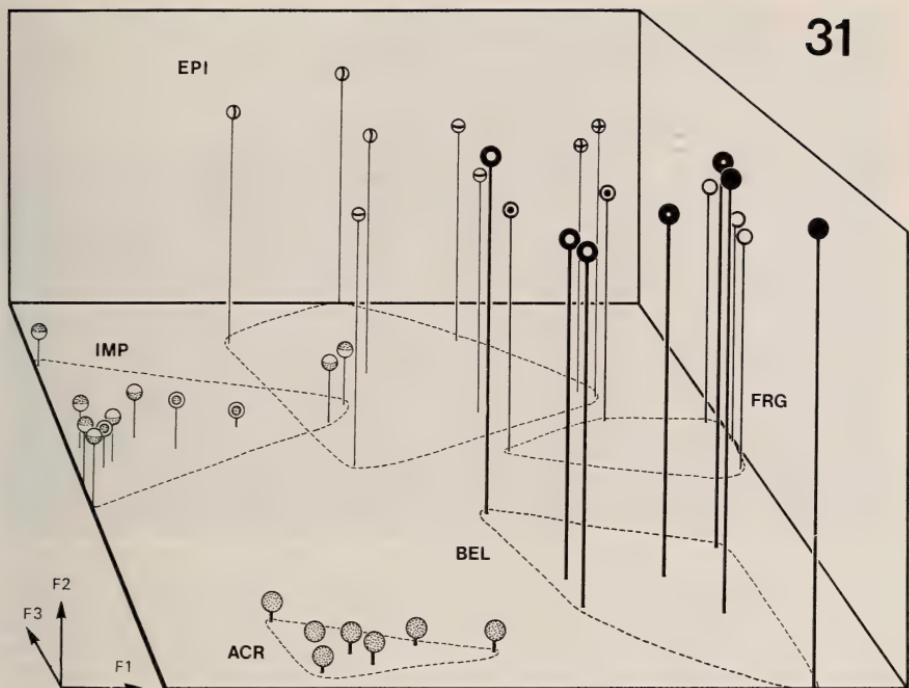
FIG. 31.   Ordination plot of male *Boloria* phenetics prepared from 75 genitalic and wing-pattern characters. Black circles, *B. bellona bellona* (filled, Indiana; small open circle, Colorado; large open circle, Connecticut). Striped circles, *B. epithore* (vertical, *chermocki*; horizontal, *borealis*; cross, *epithore*). Half-stippled circles, *B. improba* (upper-filled, *improba*; lower-filled, *youngi*; center-filled, *improbula*). Open circles, *B. frigga saga*; black center, *B. frigga sagata*. Stippled circles, *B. acrocnema*. Principal component axes indicated at lower left. Note the distinctness of species hypervolumes and semi-random assortment of subspecies within these regions.

DISCUSSION

Much slighter phenotypic differentiation over shorter geographic distances than shown by the *acrocnema-improba* pair often conceals extensive genetic divergence (e.g., Kruckeberg, 1957; Moore, 1967; Oliver, 1972, 1977; see Ayala, 1975, and White, 1978, for reviews of genetic differentiation during speciation). It is notable that Oliver (op. cit.) found considerable genetic incompatibility between geographically separated yet "phenotypically indistinguishable" populations in both *B. bellona* and *B. selene* (Schiff.) from the Nearctic region. We predict concomitant genetic differences will be found between *B. acrocnema* and *B. improba* when the appropriate biochemical and crossing analyses are conducted. We also draw attention to discordance in geographical trends among the various characters studied,
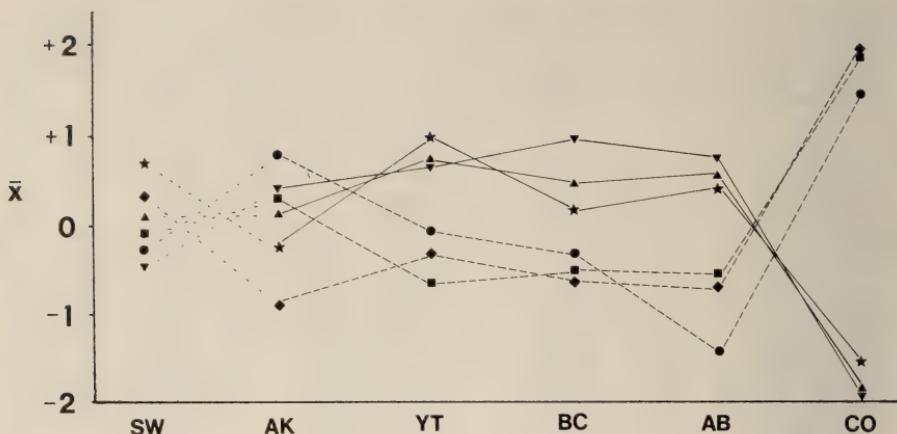
FIG. 32. Trends in means of six metric characters across the combined geographic ranges of *B. improba* (SW to AB) and *B. acrocnema* (CO). Locality abbreviations as before, except here AK refers only to northern Alaskan material. Characters 9, 12, 25, 52, R_4, and hindwing length to width ratio represented by circle, downward triangle, upward triangle, square, star, and diamond, respectively. Standardization is for graphical comparability only; see text for statistical analyses. Although discordance is extensive, note the roughly decreasing (dashed lines) and increasing (solid lines) sets of means south across the Nearctic in *B. improba*; including Coloradan *B. acrocnema* strongly *reverses* these clinal trends in each set at the Alberta–Colorado range disjunction.

(see Wilson & Brown, 1953). In certain aspects of coloration and maculation, *B. improba* from British Columbia appear superficially the closest to *B. acrocnema* in the material we have analyzed. Yet on most metric characters quantified in the text North American arctic *B. improba* are closer than are Canadian subarctic *B. improba*, with Scandinavian arctic material occupying varied positions with respect to the others (see Fig. 32). Interestingly, Scandinavian arctic *B. improba* are the most similar to *B. acrocnema* in several ventral wing-pattern characters, but, like North American arctic *B. improba*, present a general wing-pattern phenotype more divergent than Canadian subarctic *B. improba*. Local and within population variation strongly encroach upon broader geographic variation in *B. improba*, and character discordance seems to be common. The suitability of the *B. improba* trinomens as presently defined, especially in the Nearctic, therefore appears somewhat in doubt. Other multivariate work on intraspecific variation in *B. improba* generally supports this suggestion.

Little has been published on the ecology and habits of Nearctic *B. improba*, although the life history of Scandinavian arctic *B. improba* is partially known. In northwestern Finland, the presumed host (based principally on adult association) is *Salix herbacea* (L.), and

FIG. 33. Habitat of *Boloria acrocnema* on Mt. Uncompahgre, Hinsdale Co., Colorado. The view is to the SE, at elev. approx. 4100 m. Adults fly across the slopes in the immediate foreground, and to the left of the path. Oviposition activity by females on and near the Snow Willow *Salix nivalis* was most frequently observed at lower left center, in front of the lighter colored slope. Photograph by Clifford D. Ferris.

populations occur in very rocky areas with late snow melt (Bruun & von Schantz, 1948). At present only several days' observations are available for *B. acrocnema*. More detailed population studies on both species continue and will be reported elsewhere (Gall, Sperling, & Shaw, unpublished).

The colony site (Fig. 33) for *B. acrocnema* is located several hundred meters SE of the summit of Mt. Uncompahgre, elev. approx. 4080–4140 m. The path to the peak (4361 m) bisects the type locality. This area is an exposed, northeast-facing high alpine meadow. It is covered with small rocks and merges with a scree slope to the north. Both males and females were flying in modest abundance (we estimated several hundred individuals *in toto*) as early as 0800 h on 30 July 1978 under calm, sunny, but brisk conditions. A pair was taken *in copula* at 0957 h resting in the vegetation on a steep rocky slope overlooking the main site. The wing-wear condition of the adults (intermediate and worn males, fairly fresh females) suggested that the flight season was at or just beyond the median date. Mark-release-recapture data from late July and early August 1979 indicate that daily adult numbers are on the order of 150 to 180 at peak flight. Adult activity is also exceedingly localized in space, in part to an area

where the preferred oviposition substrate and larval host-plant Snow Willow (*Salix nivalis* Hook.) occurs.

Parnassius phoebus (Fabr.), *Colias meadii* Edw., *Plebejus shasta* (Edw.), *Euphydryas anicia* (Dbldy.), *Oeneis taygete* Geyer, *O. melissa* (Fabr.), *Erebia callias* Edw., and *Pyrgus centaureae* (Rambur) fly at or near the colony site. *Colias scudderi* Reakirt, *C. eurytheme* Boisd., *Lycaena cupreus* (Edw.), *Agriades glandon* (Prunner), *Boloria titania* (Esper), *B. freija* (Thunberg), *Speyeria mormonia* (Boisd.), and *Erebia theano demmia* Warren (on even numbered years) fly in more sheltered areas above timberline at elevations from 3650–3850 m.

The southernmost limit presently known for *B. improba* in the Nearctic is Prospect Mountain, 8.3 km W of Mountain Park, Alberta, elev. 2740 m. This locality itself is a modest disjunction in the Canadian subarctic range of *B. improba*, and is over 1800 km from Mt. Uncompahgre. We consider that the observed allopatry between *B. acrocnema* and *B. improba* reflects a post-Wisconsin glaciation loss of intermediate populations in a formerly more continuous distribution throughout the southern and central Rocky Mountains, and that these species have since been isolated. It seems highly unlikely that *B. acrocnema* will prove widespread in distribution, since considerable collecting has been conducted in the major high altitude parts of Colorado other than the San Juan Mountains, and in high ranges of New Mexico and Utah. Such a distinctive butterfly would not have been overlooked if present. Although to date one colony is known, we feel careful searches will probably uncover additional colonies of *B. acrocnema* in the San Juan Mountains.

We have carefully weighed the present and future conservational implications of disclosing precise locality data for the Mt. Uncompahgre population. We feel that extensive publicity of this unique, potentially fragile situation is the most positive option available for insuring a healthy future for this local endemic.[3] In the interim, pending further details on the biology and population dynamics of *B. acrocnema*, we suggest collectors remove only very small series of adults from this population. Ecological and distributional data continue to be obtained so that knowledgeable statement concerning the

Note added in proof: Mark-release-recapture data from late July and early August 1980 indicate that daily adult numbers may be of the order of up to 250 at peak flight (compared to high estimate of 180 made in 1979).

conservational status of this species can be made. The possibility of a comprehensive management plan for the diverse and scenic Mt. Uncompahgre area is also presently being considered.

LITERATURE CITED

AYALA, F. J. 1975. Genetic differentiation during the speciation process. Evol. Biol. 8: 1–78.

BROTHERS, D. J. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. Univ. Kansas Sci. Bull. 50: 483–648.

BRUUN, H. & M. VON SCHANTZ. 1948. Till kännedomen om *Brenthis improba* Btl. ssp. *improbula* Bryk. (Lepid.). Not. Ent. 29: 82–89.

BURNS, J. M. 1960. A new species of oak-eating *Erynnis* (Lepidoptera: Hesperiidae) restricted to the southern cordillera of the United States. Wasm. J. Biol. 18: 147–160.

CARDÉ, R. T., SHAPIRO, A. M. & H. K. CLENCH. 1970. Sibling species in the *Eurydice* group of *Lethe* (Lepidoptera: Satyridae). Psyche 77: 70–103.

CLENCH, H. K. 1972. *Celastrina ebenina*, a new species of Lycaenidae (Lepidoptera) from the eastern United States. Ann. Carnegie Mus. 44: 33–44.

DICE, L. R. 1943. The Biotic Provinces of North America. Univ. Mich. Press, Ann Arbor. 78 p.

DOS PASSOS, C. F. 1964. A synonymic list of the nearctic Rhophalocera. Mem. Lepid. Soc. 1: 1–145.

——— & L. P. GREY. 1945. A genitalic survey of Argynninae (Lepidoptera: Nymphalidae). Amer. Mus. Novitates 1296: 1–29.

EHRLICH, P. R. & H. K. CLENCH. 1960. A new subgenus and species of *Callophrys* (s.l.) from the southwestern United States (Lepidoptera: Lycaenidae). Entomol. News 71: 137–141.

——— & A. H. EHRLICH. 1967. The phenetic relationships of the butterflies. I. Adult taxonomy and the nonspecificity hypothesis. Syst. Zool. 16: 301–317.

FREEMAN, T. N. 1956. The distribution of arctic and subarctic butterflies. Proc. Tenth Int. Congr. Ent. 1: 659–672.

GALL, L. F. 1976. The status of *Satyrium boreale* (Lycaenidae). J. Lepid. Soc. 30: 214–218.

HARMAN, H. H. 1976. Modern Factor Analysis. Univ. Chicago Press, Chicago. 487 p.

HENNIG, W. 1966. Phylogenetic Systematics. Univ. Ill. Press, Urbana. 263 p.

HIGGINS, L. G. & N. D. RILEY. 1970. A Field Guide to the Butterflies of Britain and Europe. Collins, London. 380 p.

KLOTS, A. B. 1951. A Field Guide to the Butterflies of North America, east of the Great Plains. Houghton Mifflin, Boston. 349 p.

———— 1956. Lepidoptera, pp. 97–111. In S. L. Tuxen [ed.], Taxonomists' Glossary of Genitalia in Insects. Munksgaard, Copenhagen.

KRUCKEBERG, A. R. 1957. Variation in fertility of hybrids between isolated populations of the serpentine species, Streptanthus glandulosus Hook. Evolution 11: 185–211.

LAFONTAINE, J. D. 1970. A redescription of Strymon borealis Lafontaine (Lycaenidae). J. Lepid. Soc. 24: 83–86.

MAYR, E. 1963. Animal Species and Evolution. Belknap, Harvard Univ. Press, Cambridge. 797 p.

———— 1974. Cladistic analysis or cladistic classification? Zeit. fur Zool. Syst. und Evol. 12: 94–128.

MICHENER, C. D. 1970. Diverse approaches to systematics. Evol. Biol. 4: 1–38.

MOORE, J. A. 1967. Diploid and haploid hybridization of different populations of the Rana pipiens complex. J. Exp. Zool. 165: 1–20, 461–474.

OLIVER, C. G. 1972. Genetic and phenotypic differentiation and geographic distance in four species of Lepidoptera. Evolution 26: 221–241.

———— 1977. Genetic incompatibility between populations of the nymphalid butterfly Boloria selene from England and the United States. Heredity 39: 279–285.

PARKS, J. M. 1968. Classification of mixed-mode data by R-mode factor analysis and Q-mode cluster analysis on distance function, pp. 187–192. Proc. Colloquium in Numerical Taxonomy, Univ. of St. Andrews.

———— 1970. FORTRAN IV program for Q-mode cluster analysis on distance function with printed dendrogram. Kansas Geol. Survey Computer Contrib. 46: 1–32.

PERKINS, E. M. & W. C. MEYER. 1973. Revision of the Boloria epithore complex, with description of two new subspecies (Nymphalidae). Bull. Allyn Mus. 11: 1–23.

PIKE, E. M. 1978. Origin of tundra butterflies in Alberta. MS Thesis, Univ. of Alberta, Edmonton. 137 p.

REMINGTON, C. L. 1968. A new sibling Papilio from the Rocky Mountains, with genetic and biological notes (Insecta, Lepidoptera). Postilla 119: 1–40.

ROHLF, F. J. 1968. Stereograms in numerical taxonomy. Syst. Zool. 17: 246–255.

———— & R. R. SOKAL. 1969. Statistical Tables. Freeman, San Francisco. 253 p.

SNEATH, P. H. A., & R. R. SOKAL. 1973. Numerical Taxonomy: the principles and practice of numerical classification. Freeman, San Francisco. 573 p.

SOKAL, R. R. 1975. Mayr on cladism—and his critics. Syst. Zool. 24: 257–262.

———— & F. J. ROHLF. 1969. Biometry. Freeman, San Francisco. 776 p.

STALLINGS, D. B. & J. R. TURNER. 1954. Notes on Megathymus neumoegeni, with description of a new species (Megathymidae). Lepid. News. 8: 77–87.

WARREN, B. C. S. 1944. Review of the classification of the Argynnidi: with a systematic revision of the genus Boloria. Trans. Roy. Entomol. Soc. London 94: 1–101.

WHITE, M. J. D. 1978. Modes of Speciation. Freeman, San Francisco. 455 p.

WILSON, E. O. & W. L. BROWN, JR. 1953. The subspecies concept and its taxonomic application. Syst. Zool. 2: 97–111.

APPENDIX
Characters employed in phenetic analyses[1]

Character description[2]	Number of states[3]	Character weighting[4]	Character description[2]	Number of states[3]	Character weighting[4]
MALE GENITALIC CHARACTERS			35. Intensity of maculation distad from FW subbasal area	4	1
1. Length of aedeagus	C	1	36. Extent of whitish suffusion on FW	3	2
2. Length: width ratio of aedeagus	C	1	37. Proportion of submarginal spots in cells	3	3
3. Shape of caecum	2	3	38. Width 5th: width 2nd FW postmarginal spots	C	1
4. Basal width of ductus ejaculatorius	C	1	39. Relative size progression of postmarginal spots	3	2
5. Shape of rostellum	3	2	40. Length from margin to postmarginal spot in cell R_4	C	1
6. Length of digitus	C	3			
7. Width of digitus at distal end	C	1	41. Length from margin to postmarginal spot in cell M_2	C	1
8. Width of digitus at center	C	2	42. Shape of FW basal spot	3	3
9. Length digitus: length valve	C	3	43. Width postmedian band in cell M_3	C	1
10. Shape of digitus spines	4	3	44. Distance from subapical spot to terminal postmarginal spot in cell R_2	C	2
11. Number of digitus spines	3	1			
12. Length of uncus	C	3	45. Confluence of FW bands distad from subbasal area	3	3
13. Length: width ratio of uncus	C	1	46. Number open centered spots along costal margin	4	3
14. Length uncus: length valve	C	1	47. Disjunction of FW postmedial band in lower limbal area	5	1
15. Degree of uncus curvature	2	2			
16. Shape of caudal section of tegumen	3	3	48. Angle of 3rd FW costal spot	3	3
17. Width of tegumen at center	C	1	49. Antenna length	C	2
18. Degree of tegumen curvature	2	2	50. Length of antennal club	C	1
19. Length of dorsal arm of cucullus	C	1	51. Length: width of antennal club	C	1
20. Shape of distal section of cucullus	3	2	52. Length: width of FW	C	3
21. Terminal prong shape on cucullus	3	2	**VENTRAL WING-PATTERN CHARACTERS**		
22. Number of teeth on dorsal arm of cucullus	4	2			
23. Length of valve	C	3	53. FW ground color[5]	4	2
24. Angle formed by harpe and costal arm	3	2	54. Degree of contrast in FW maculation[5]	3	2
25. Width of saccus	C	3	55. Separation of FW postmedial spots in upper limbal area[5]	3	1
26. Width of saccus: valve length	C	1	56. Maculation contrast in HW discal area	4	3
27. Shape of distal part of saccus	3	2	57. Extent of purplish cast on HW	3	3
28. Width of costal arm	C	2	58. Form of postmedian-median HW row	4	3
29. Costal arm width: digitus length	C	2	59. Extent of white-silver on postmedian-median HW row	5	2
30. Costal arm width: valve length	C	3	60. Shape HW white costal spot	2	3
DORSAL WING-PATTERN CHARACTERS			61. Coloration at FW apex[5]	2	1
			62. Contrast FW veins with ground color	3	2
31. Forewing ground color	4	2			
32. Degree of contrast in FW maculation	3	3			
33. Extent of HW melanization	4	2			
34. Extent of HW submedial spot	3	2			

APPENDIX
Continued

Character description[2]	Number of states[3]	Character weighting[4]	Character description[2]	Number of states[3]	Character weighting[4]
63. Shape of wing margins	3	2	71. Length of postmedian-median row discal spot: FW length	C	2
64. Forewing length	C	2			
65. Relative width of FW maculation along costa	3	2	72. Amount of darker coloration marginad of FW marginal spots	3	3
66. Form of HW margin spots & fringe[5]	3	2	73. Amount of darker coloration distad of FW marginal spots	3	1
67. Color of FW veins[5]	3	2			
68. Form of white spot basad of HW costal spot	4	1	74. Ground color shift above M_2 near submarginal spots	3	1
69. Offset of postmedian-median row below discal cell	3	1	75. Color of palpi on under-surface	4	2
70. Length of postmedian-median row discal spot	C	1			

[1] The set of wing-pattern characters is a composite of those compiled in 1978 by us and others compiled more recently by students in an undergraduate evolutionary biology laboratory at Yale University. An array of male *Boloria* was given to them as an exercise in phenetic taxonomy (with no further instructions); their data returned a phenogram and ordination plot comparable to earlier versions obtained with our data. Of their 44 characters, 18 proved to be identical to ones we had used earlier; these were discarded, and the remaining 26 appended to our original list.

Characters were scored on the right side of genitalia (ventral view) and right wings, whenever possible. Fifty-nine missing values (e.g., no antennae) were encountered, representing 1.4% (59 of 4275) of the cells in the data matrices. These cells were filled with the means from larger samples for that population or immediate geographic region.

We also caution here against a potential complication inherent in mixing ratios and size-scaled variables with raw dimensions in multivariate analyses. Ratios and size-scaled variables sometimes exhibit non-linear relationships which may distort linear matrix analyses, such as principal components (see, for example, the journal *Systematic Zoology* [vol. 27, pp. 61–83; 1978] for diverse opinions on this subject). Since discussing the effects of such mixing is beyond the scope of this paper, we simply note that phenograms based on the sets of characters excluding ratios and size-scaled variables returned identical taxonomic decisions.

[2] Terminology follows dos Passos & Grey (1945) and Klots (1956).

[3] A "C" indicates a continuous variable; full character state descriptions are available from the senior author upon request.

[4] Number indicates principal component in ordination plot on which this character is most heavily weighted (these are ranked factor loadings of the original characters; see Fig. 31).

[5] Indicates characters not scored in females.

GENERAL NOTES

THE GENUS *CHLOROSTRYMON* AND A NEW SUBSPECIES
OF *C. SIMAETHIS*

In 1961 Harry Clench (*in* Ehrlich & Ehrlich, How to know the butterflies, Dubuque, Iowa, 262 p.) erected a new genus *Chlorostrymon* and selected as type species *Thecla telea* Hewitson. His description of the genus was very brief. Current authors consider this a valid genus and I feel that the generic description should be elaborated upon to provide a more definitive picture of the taxa contained therein.

Genus Chlorostrymon Clench, 1961

Type species: *Thecla telea* Hewitson, 1868.

Description. Hindwing tailed, usually two, the shorter (at times rudimentary or missing) at the end of Cu_1, the second always present at the end of Cu_2. **Upper wing** surfaces iridescent lavender-blue in the male, brown with pale blue scaling at the wing bases in the female; the underside of the wings, green. **Eyes** densely covered with short, pale bristles; **palpi** short, scaled, porrect, terminal segment short. The **antennae** one-half the length of the forewing costa, the club formed rather abruptly, the nudum completely bare only on the 3 terminal segments.

Genitalia. Male genitalia with a wide, short saccus, the valvae completely separate throughout, the aedeagus complex, relatively stout, inordinately large with a ventral keel and with the terminal one-quarter clearly separated from the main shaft, but attached by a narrow transparent membrane and a heavy, long sharp cornutus which traverses the break. **Female bursa copulatrix** with a funnel-shaped ostium bursae, the dorsal plate lightly sclerotized, convex, centrally divided, the ventral portion a short membraneous pouch; the ductus bursae relatively long, chitinous, the terminal one-quarter sharply bent dorsally 90°, the cervix bursae a fan-shaped opening into the corpus bursae with a pair of small, dark, sclerotized, rough-surfaced pads located dorsad to the entry of the ductus seminalis. The corpus bursae longer than the complete bursa copulatrix and with two small, simple, blunt, tooth-like signa.

Remarks. The species currently recognized as belonging to *Chlorostrymon* are *telea* (Hewitson), *maesites* (Herrich-Schaffer) and *simaethis* (Drury). Each has been discussed and well illustrated in recent publications, e.g., Klots (1951, A field guide to the butterflies, Boston, 349 p.), Barcant (1970, Butterflies of Trinidad and Tobago, London, 314 p.), Lewis (1974, Butterflies of the world, Chicago, 312 p.), Riley (1975, A field

FIG. 1. **A,** *Chlorostrymon simaethis rosario* Nicolay, Holotype ♂, La Kenedy, Pichincha, Ecuador (2800 m), May 1969 (Rosario Lafebre); **B,** underside of A.
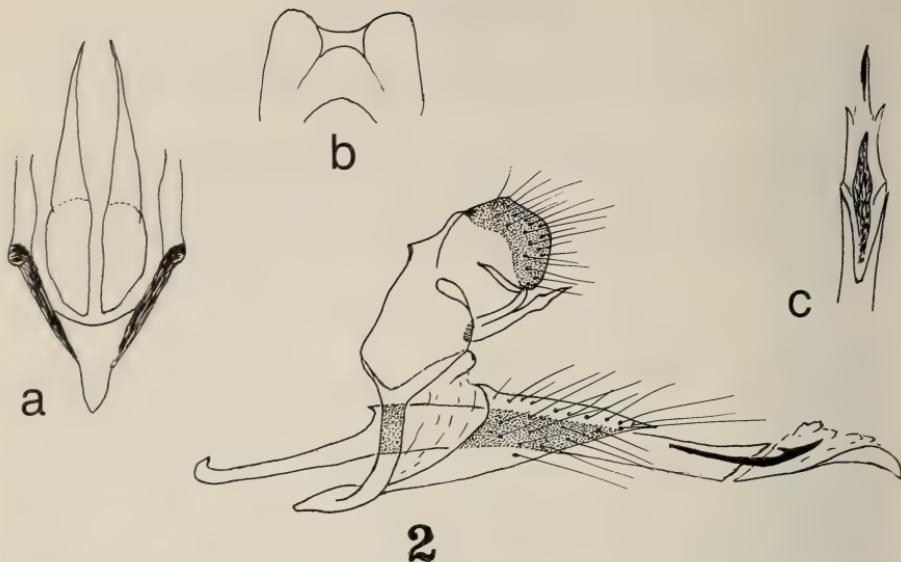
FIG. 2. Male genitalia of *C. simaethis rosario* Nicolay, lateral view with aedeagus in place; **a,** ventral view of saccus with valve in place; **b,** dorsal view of uncus; **c,** ventral view of aedeagus termen.

guide to the butterflies of the West Indies, Collins, London, 224 p.), Thorne (1975, *in* Howe, The butterflies of North America, New York, 633 p.). To further document individual taxa here would serve no useful purpose. They are all essentially tropical and are found widely distributed throughout both North and South America. A number of subspecies have been described and recent collecting in Ecuador has revealed a new subspecies of *C. simaethis,* described below.

Chlorostrymon simaethis rosario Nicolay, new subspecies
Figs. 1A, 1B, 2, 3

Description. Male: Length of forewing, 11 mm. **Upperside:** forewing violet-blue in the discal area, with wide, darker costal, apical and outer wing borders, the colors blending smoothly without a sharp line of demarcation. **Hindwing** the same violet-blue, but more intense, the dark borders somewhat narrower. Anal lobe spot reddish-brown tipped in black. Fringes on hindwing noticeably pale. A short, spike-like tail at Cu_2 and a rudimentary spur at Cu_1. **Underside:** forewing yellow-green along a wide band from the base along the costal margin including the apex to Cu_2; below this to the inner margin, pale grey. A straight, narrow silvery-white macular postmedian line extends from the coastal margin to Cu_1, the line narrowly edged on both sides by pale brown scales. **Hindwing** green with a straight, narrow silvery-white macular line of spots, bisecting the very center of the wing disc from the costal margin to vein 2A where it turns sharply to the inner margin. A narrow marginal band of soft, pale grey-brown begins at the wing apex and broadens to its widest expanse and terminus at vein 2A. Small patches of silvery scales are dusted along the inner edge of this outer marginal band, along with small scattered spots of dark brown scales, the heaviest concentration at interspace 2A. The anal lobe spot is brown. **Abdominal, thoracic, palpi and leg scales** on the underside grey-white. Antennae checked black and white, the relatively heavy club of 13 segments sharply delineated.

Female. Expanse of forewing, 11 mm. **Upperside** pale brown with sparse pale
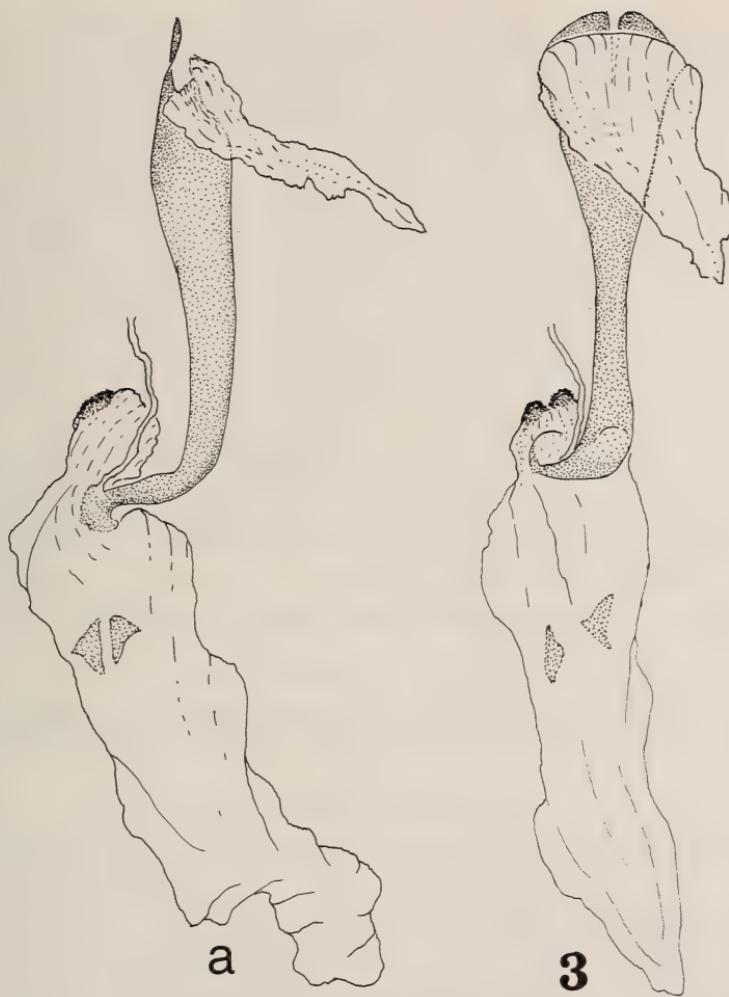
FIG. 3. Female genitalia of *C. simaethis rosario* Nicolay, ventral view; **a,** lateral view.

blue scaling confined to the base of both fore- and hindwings. **Underside** yellow-green as in the male, the white postdiscal line of the forewing, narrow, curved slightly basad. The postdiscal white line of the hindwing narrow, straight from the costa to below the cell where it turns slightly basad, then straight again to vein 2A, then sharply angled to the inner margin. The outer marginal grey band as in the male.

Types. Holotype ♂, La Kenedy, Pichincha, Ecuador (2800 m) May 1969, collector, Rosario Lafebre. Paratypes include 11 ♂ from the type locality with dates in December 1968. The Allotype, a very worn ♀ from San Bartolo, March 1969 (2800 m), collector, Rosario Lafebre. The Holotype ♂ and Allotype ♀ with 10 ♂ Paratypes are located in the Allyn Museum of Entomology, Sarasota, Florida. A single ♂ paratype is in the author's collection.

Etymology. It is a pleasure to name this interesting subspecies after Rosario Lafebre of Quito, Ecuador, a friend and an ardent butterfly collector for many years.

Remarks. The number of named subspecies of *Chlorostrymon simaethis* now is four. When specimens are viewed from above, it is difficult to make a positive identification of any subspecies. All are essentially identical, with the possible exception of size, which may or may not be associated with different localities. Subspecific differences from the nominate *simaethis* are located on the underside of the wings, and concern primarily the differences in the discal lines. Typical *simaethis* has the postdiscal of the forewing bending inward, and that of the hindwing uneven throughout its entire length. The subspecies *sarita* Skinner (1895, Ent. News, 6: 112, Philadelphia) has the postdiscal of the forewing somewhat straighter, and that of the hindwing curved slightly basad with an obvious "bulge" outward at about the midpoint of the wing. The subspecies *jago* Comstock & Huntington (1943, Lycaenidae of the Antilles, Ann. New York Acad. Sci. p. 49–130) appears to be a minor variation of typical *simaethis*; it is considerably larger and the narrow, uneven maculation of the underside is thus magnified. *C. simaethis rosario* follows this varietal pattern on the underside; the discal line is very straight, very narrow without any 'bulge' and the marginal grey band is rather narrow. As a result, the wing has a greater expanse of green color between the discal band and the marginal band.

The Allyn Museum collection contains series of *simaethis* and its subspecies from various tropical localities in the hemisphere. Careful scrutiny of the undersides of any series from a single locality reveals an extraordinarily variable insect. The subspecies *sarita*, found throughout Central and South America from Mexico to Argentina, is the most variable of all. This variability is found within series from any particular locality, and is not correlated with geography.

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OVIPOSITION BEHAVIOR OF REARED *ANTHERAEA POLYPHEMUS* (SATURNIIDAE)

To improve efficiency in the collection of eggs, we studied oviposition behavior in the giant silkworm moth species we rear. We reported information for *Callosamia promethea* (Drury) (Miller & Cooper 1977, J. Lepid. Soc. 31: 282–283) and *Hyalophora gloveri gloveri* (Strecker) (Miller 1978, J. Lepid. Soc. 32: 233–234). Taschenberg & Roelofs (1970, Ann. Entomol. Soc. Amer. 63: 107–111) have reported information for *Hyalophora cecropia* (Linnaeus). This paper reports oviposition data for a colony of *Antheraea polyphemus* (Cramer) maintained on various maples (*Acer* spp.) in Frederick Co., Maryland.

The adult moths in the colony typically emerged in the late afternoon or early evening (1600–1900 hours). If male moths were in the colony, they were placed with the females in indoor mating cages; if males were not available, we placed the females in outdoor mating cages (Miller & Cooper 1976, J. Lepid. Soc. 30: 95–104) to attract wild males for copulation. Only females that mated on the night of or following emergence were included in this study. Mating pairs were observed at frequent intervals
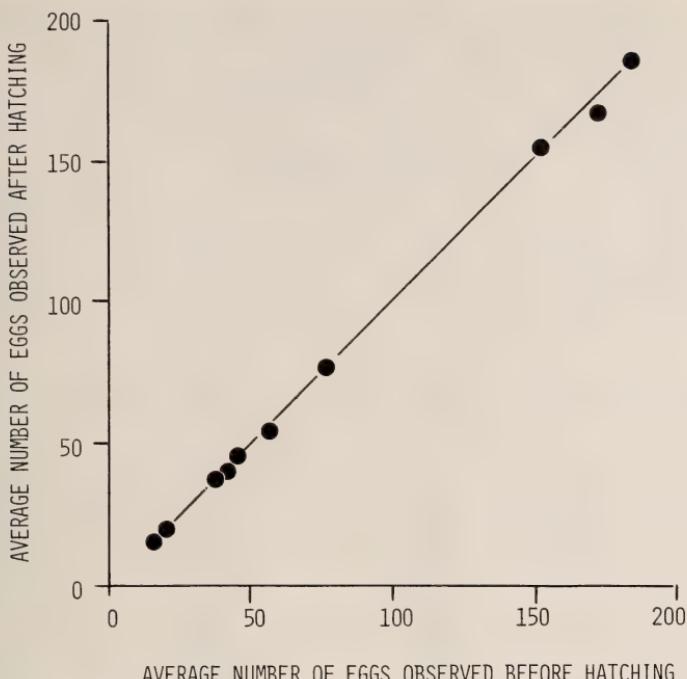
FIG. 1. Relationship between *Antheraea polyphemus* egg counts made before hatching and after hatching and larval feeding on shells.

and females were placed in brown paper bags (lunch size) for oviposition as soon as the mated pairs separated. Females were transferred to new paper bags each night until death. We collected eggs from 16 *A. polyphemus* females.

After a period of time sufficient to allow all eggs to hatch, the bags were opened to record the number of eggs deposited and the number hatched. We observed that larval feeding on egg shells had reduced many egg shells to a very small piece attached to the bag. When larvae hatch in the oviposition bags with foodplants present, they move to the plants and normally do not return to the paper surfaces to consume the egg shells. Allowing the larvae to hatch in bags in the absence of foodplants apparently resulted in more frequent consumption of egg shells. It is thus possible that some eggs might be consumed and lost from the data set. To examine this possibility, we randomly selected 10 oviposition bags. We counted the eggs twice: once before hatching and again after the eggs had hatched and the larvae had fed on the egg shells. The eggs in each bag were counted by each of us before and after hatching.

Fig. 1 shows that the relationship between counts made before and after hatching is linear in our random sample (18–187 eggs per bag). The differences between paired counts averaged less than 1%. We conclude that larval feeding did not adversely affect the accuracy of egg counts made after hatching.

While determining the number and percent hatch of eggs from the 16 females, we observed a very low percent hatch (27.0 and 60.4 percent) for eggs from two individuals that had mated with reared males. Of the 16 females, 8 had mated with reared males and 8 with wild males. To examine the possibility that the type of male was a factor in the number of eggs deposited or the percent hatch, we compared the oviposition and hatching data for these two groups of females (Table 1). Since low percent hatch

TABLE 1. Oviposition and hatching data for eggs from *Antheraea polyphemus* females mated with reared males or wild males.

| Female number | Number of eggs | | Percent hatch |
	Deposited	Hatched	
	Mated with Reared Males		
1	84	84	100.0
2	200	54	27.0
3	138	133	94.9
4	172	169	98.2
5	253	153	60.4
6	264	263	99.6
7	357	353	98.8
8	177	174	98.3
	1645	1381	83.9
	Mated with Wild Males		
1	199	187	93.9
2	249	236	94.7
3	226	210	92.2
4	189	181	95.7
5	242	240	99.1
6	225	222	98.6
7	269	262	97.3
8	227	223	98.2
	1826	1761	96.4
Totals	3471	3142	90.5

was not consistent among females mated with reared males, we conclude it is not attributable to the reared males. It is possible that the two females in question were involved in sibling matings. However, since we do not maintain individual broods separately we cannot determine this. Low percent hatch for eggs from certain females is a characteristic of the colony; determining the cause is not critical to elucidating the oviposition pattern for our purposes. Therefore, we have consolidated the oviposition and hatching data for all 16 females (Table 2) to accurately represent the oviposition

TABLE 2. Summary of oviposition and hatching data for eggs from reared *Antheraea polyphemus* females.

| Night after mating | Number of females | Eggs deposited | | % Hatch |
		Number	Cumulative %	
1	16	2030	58.5	91.0
2	16	706	78.8	91.6
3	16	358	89.1	90.2
4	16	176	94.2	88.0
5	15	148	98.4	88.5
6	10	38	99.5	76.3
7	5	14	99.9	64.0
8	3	1	100.0	0
9	0	0	100.0	0

behavior of this *A. polyphemus* colony. These 16 individuals deposited a total of 3471 eggs over a 9-day period. All females survived for at least 4 days after mating; 3 individuals lived for 8 days. The average longevity after mating was 6.1 days. The maximum number of eggs deposited by a single female that lived for 8 days was 357; the minimum number was 84 for a female that lived for 4 days. The average number of eggs deposited per female was 216.9. Average percent hatch decreased gradually with time after mating of the females, with a marked decrease after the fifth night.

From these observations we conclude: 1) feeding on egg shells by *A. polyphemus* larvae after they hatch does not adversely affect the collection of oviposition data; 2) whether or not a female *A. polyphemus* mates with a reared male or a wild male does not appear to influence either the total number of eggs deposited or the percent hatch; and 3) *A. polyphemus* follows the general pattern reported for other giant silkworm moth species (the optimum period for collecting eggs is during the first three nights after mating).

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[1] Entomologist & Research Chemist, respectively; the opinions contained herein are those of the authors and should not be construed as official or reflecting the views of the Department of the Army.

NATURAL INTERSPECIFIC PAIRING BETWEEN *PIERIS VIRGINIENSIS* AND *P. NAPI OLERACEA* (PIERIDAE)

Recent records for *Pieris napi oleracea* Harris and its congener *P. virginiensis* Edw. confirm that although the latter has a more southerly distribution, the geographic ranges of these two species overlap widely in the northeastern United States and upper Great Lakes region (e.g., Forbes 1960, Lepidoptera of New York and neighboring states, Part IV, Cornell Univ. Agric. Expt. Sta., Ithaca, New York; Muller 1968, J. New York Entomol. Soc. 76: 303–306; Tasker 1975, J. Lepid. Soc. 29: 23; Shull 1977, ibid., 31: 68–70; Wagner & Mellichamp 1978, ibid., 32: 20–36; Drees & Butler 1978, ibid., 32: 198–206). The two species are ecologically as well as morphologically distinct. The univoltine habit of *P. virginiensis* corresponds well with the vernal phenology of its woodland larval foodplant (*Dentaria* spp., primarily *D. diphylla* Michx.), although some potential for polyphenism exists (Shapiro 1971, Ent. News 82: 13–16). *P. n. oleracea* is usually bi- (sometimes tri-) voltine and occupies a variety of habitats. These include the beech-maple-hemlock woods in which *P. virginiensis* may be found (where *P. n. oleracea* also utilizes *Dentaria* spp. as a larval foodplant) as well as other wooded areas (e.g. tamarack bog, Shull 1977, op. cit.; *Thuja occidentalis* swamp, Chew 1978, J. Lepid. Soc. 32: 129) and open areas where it exploits several native and naturalized crucifer species as larval foodplants (Chew 1978, Atala 5: 13–19).

Despite the geographic overlap of these species, however, sympatry on a local scale seems to be rather uncommon, with the result that members of these two species do not frequently interact. Known areas of local sympatry are southern Vermont, western Massachusetts (Howe 1975, The butterflies of North America, Doubleday, Garden City, New Jersey; A. B. Klots, in litt.) and northern Michigan (Wagner, in litt. and 1956,

FIG. 1. *Pieris virginiensis* ♀ (right) × *P. napi oleracea* ♂ (left). Wahconah Falls State Park (Berkshire Co.), Massachusetts, 8 May 1979, 1110–1124 EDT, leg. F. Chew. Note that the suffused, "smoky" appearance of the HW underside of *P. virginiensis* contrasts with the sharp, intense melanic markings on the HW underside of the spring brood of *P. n. oleracea*. Photograph by Jason Weintraub.

Lepid. News 10: 18–24). In western Massachusetts near Dalton (Berkshire Co.), both species fly in beech-maple-hemlock woods where *Dentaria diphylla* Michx. is abundant. On 8 May 1979, a clear, calm day (ca. 22°C), M. Deane Bowers, Ira M. Heller, Jason Weintraub and I visited Wahconah Falls State Park near Dalton. We saw several *P. virginiensis* females and several worn *virginiensis* males. We also saw about a dozen fresh *P. n. oleracea* males but failed to find any *oleracea* females. About 1030 h, Deane Bowers saw an interspecific pairing (*virginiensis* ♀ × *oleracea* ♂). This pair eluded capture. We saw a second such pairing at 1110; it is possible that a single pair was seen twice. We also saw a *virginiensis* × *virginiensis* pairing at 1324.

The second interspecific pair (Fig. 1) was captured and remained coupled until 1124. The female was later placed in a small net cage over *Dentaria diphylla* leaves under Sylvania fluorescent "Cool White" and "Gro-lux" lights. After a two day delay, the *virginiensis* female laid 18 eggs over the succeeding eight days. These eggs were kept in a humidified incubator at 19°C; other *virginiensis* and *napi oleracea* eggs hatched in 5–6 days under these conditions. After more than three weeks, some of the *virginiensis* × *oleracea* eggs collapsed. None hatched. Dissection of the *virginiensis* female later revealed that her body contained a single spermatophore.

These pairings are of interest not only because they involve non-conspecific individuals, but also because the individuals represent closely related native species which maintain distinctness in sympatry as well as allopatry (Klots 1951, A field guide to the butterflies, Houghton Mifflin, Boston; Ehrlich & Ehrlich 1961, How to know the butterflies, Brown, Dubuque, Iowa; Howe, 1975, op. cit.; Lorkovic 1978, Acta entomologica Jugoslavica 14: 13–24). Natural interspecific pairings between native Nearctic *Pieris* and the naturalized *Pieris rapae* (e.g., Scudder 1889, Butterflies of New England,

Boston, p. 1212; Priestaf 1972, J. Lepid. Soc. 26: 104) may reflect the relatively recent introduction of *P. rapae* to North America and its subsequent geographic overlap with native *Pieris* (Scudder 1889, loc. cit.; Klots 1951, loc. cit.). The possibility that crosses between *P. virginiensis* and *P. n. oleracea* from this locality are fertile can be tested using laboratory-reared stock. Bowden (in litt. and 1972, Proc. Brit. Entomol. Nat. Hist. Soc. 4: 103–117) found that some crosses between *virginiensis* and *napi oleracea* individuals (from stocks from different localities) produced viable hybrid offspring (tests of hybrid fertility were negative but too few to be conclusive); others produced infertile eggs. If the artificial crosses produce fertile hybrid offspring, then one might expect to find some evidence of introgression in sympatric populations (cf. Hovanitz 1963, J. Res. Lepid. 1: 124–134). If the crosses are not fertile, then the observation that these two distinct, sympatric, native *Pieris* do not exhibit more effective pre-zygotic isolating mechanisms is curious (cf. Shapiro 1975, Am. Midl. Nat. 93: 424–433).

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UTILIZATION OF GRASS INFLORESCENCES AS ADULT RESOURCES BY RHOPALOCERA

Adult Lepidoptera utilize a number of energy sources to supplement the nutritive material assimilated during the larval stage. While flower nectar is the most common adult resource, others, e.g., rotting fruit, carrion and dung are often utilized (Downes 1973, J. Lepid. Soc. 27: 89–99; Neck 1977, J. Res. Lepid. 16: 147–154). Flowers most frequently visited are those with colorful petals and/or sepals. While tropical grasses are visited by a large number of insect species (Soderstrom & Calderon 1971, Biotropica 3: 1–16), as a general rule, grasses have non-conspicuous, anemophilous flowers which have few, if any, insect visitors.

Herein I report massive utilization of grass inflorescences by several species of Rhopalocera. Observations were made along Sandy Creek in Enchanted Rock State Park, Llano Co., Texas, on 27 October 1978 from 1000 to 1700 h. Skies were cloudless; temperature range was 10°–25°C during the observation period.

Rhopalocera were visiting inflorescences of two grass species: K-R bluestem, *Bothriochloa ischmaeum* (L.) Keng var. songarica (Fisch & Mey.) Celarier and Harlan, and Dallis grass, *Paspalum dilatatum* Poir. The following species and numbers were observed during a single transect: *Precis coenia* (Hübner) (51), *Danaus gilippus strigosus* (Bates) (8) and *Cynthia cardui* (L.) (2). Butterflies had their probosces extended towards and around the base of achenes of the inflorescences. Achenes of both these grass species were post-anthesis, but some substance was apparently being removed from the shiny surface of the achenes.

Other rhopaloceran species present at this site but not observed at the grass inflorescences were *Anaea andria* Scudder, *Ancyloxypha numitor* (Fabricius), *Atlides halesus corcorani* Gunder, *Chlosyne lacinia* var. adjutrix (Scudder), *Colias (Zerene) caesonia* Stoll, *Colias eurytheme* Boisduval, *Eurema nicippe* (Cramer), *Nathalis iole* Boisduval, *Physiodes phaon* Edwards and *Phyciodes vesta* Edwards. Most of these species flew over the two grasses with no evidence of attraction. Butterfly families represented by the above species include Hesperiidae, Lycaesidae, Nymphalidae and

Pieridae. These butterfly species visited a number of flowering plants, e.g., *Eupatorium havanense* H.B.K. (Compositae), at which no *Precis, Danaus* or *Cynthia* were observed.

The grass-visiting species ignored not only various other flowering plants but also a number of other grass species, e.g., side-oats gramma, *Bouteloua curtipendula* (Michx.) Torr., most of which was brown with achenes fully desiccated. The stage of desiccation, i.e. maturation of seed, is the apparent key factor in restricting butterflies to the two species of grass. Both the grass species visited by Rhopalocera are weedy, drought-resistant, naturalized grasses which have extended seed production compared to native grasses (pers. obs.). *B. ischmaeum* also grows in nearly monospecific meadows on interstream high areas and terraces. A few butterflies visited inflorescences in these areas, but their numbers were not comparable to the lower sites. While arborescent vegetation at these higher sites may have restricted butterfly access, some butterflies were present; the probable reason for reduced utilization was low soil moisture which caused more rapid achene maturation. The observation of three *Precis* in immediate proximity to each other on one particularly "green" *Paspalum* inflorescence supports this idea.

Of interest is the identity of the substance obtained by *Precis, Danaus* and *Cynthia* from the surface of the achene of *Bothriochloa* and *Paspalum.* Lepidopteran adults have long been known to feed at sap exudates and honeydew on leaves (Norris 1936, Trans. R. Entomol. Soc. Lond. 85: 61–90). Karr (1976, Biotropica 8: 284–285) reported unidentified moths feeding at a "nectar-like material" of a grass species in the Canal Zone (Panama); a later report (Pohl et al. 1979, Biotropica 11: 42) indicated this substance may have involved nectar-like production by an ergot. However, I have observed several species running prosces over the surface of apparently healthy leaves without honeydew deposits or fungal infestation. Obviously, some exuded substance on the leaf or achene surface has some attractive (and presumed nutritive) value to a number of adult Rhopalocera. Grass species with extra-floral nectaries are unknown (Pohl et al., op. cit.). One wonders whether the substance(s) involved are secondary compounds produced to deter herbivory (see Levin 1976, Annu. Rev. Ecol. & Syst. 7: 121–159). However, water-soluble compounds, e.g., sugars and amino acids, are normally not present on such external surfaces. Water-insoluble compounds, e.g., waxes, flavonoid phenolic compounds and terpenoids, often occur on these external surfaces. These compounds are not nutritive in nature, however; normally they serve as feeding and/ or ovipositional deterrents or attractants. At this point one does not know whether these butterflies were obtaining a nutritive substance or were merely being stimulated by surface phytochemicals.

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(Information for Contributors may be found on inside back cover of Volume 34, Number 1.)

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HARRY KENDON CLENCH
MEMORIAL ISSUE

JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

THE LEPIDOPTERISTS' SOCIETY

The object of the Lepidopterists' Society, which was formed in May, 1947 and formally constituted in December, 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

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Cover illustration: Mature larva of *Ornithoptera goliath* Oberthür eating through the thick, corky stem of *Aristolochia crassinervia*, consuming the higher concentrations of secondary plant compounds that the stem of this vine contains. Original drawing by Mr. Michael J. Parsons, F.R.E.S., Hurst Lodge, Hurst Lane, Egham, Surrey TW20 8QJ, England.

ORIGIN OF THE LEPIDOPTERA, WITH DESCRIPTION OF A NEW MID-TRIASSIC SPECIES AND NOTES ON THE ORIGIN OF THE BUTTERFLY STEM

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ABSTRACT. Part I presents data on two new fossil wing impressions, identified as early Lepidoptera of a homoneurous type, from the Insect Bed at Mount Crosby, Queensland, now recognized to be of Mid-Triassic age. They represent a new family, the Eocoronidae, a new genus, *Eocorona*, and species, *iani*.

The status of a previously described genus and species from the same horizon in Triassic time, *Eoses triassica* Tindale, 1945 is examined and evidence given for its validity as a member of the Lepidoptera. Evolution of the homoneurous stem of the Lepidoptera is discussed in light of several living members of the family Lophocoronidae (Common, 1973), the Agathiphagidae (Dumbleton, 1952), and the recent finding of *Neotheora* in Brazil (Kristensen, 1978).

Part II offers observations on the origin of the Rhopalocera stem of the Lepidoptera, based in large part on study of tracheal systems in the wings of newly formed pupae of several superfamilies. The observations lead to the conclusion that the Butterfly stem may be rather closely linked with an ancestral line of the Castnioidea, or Butterfly-moths.

The recent discovery (Durden & Rose, 1978) of Mid-Eocene butterflies of two existing families reinforces earlier ideas that the origin of the stem should be sought in the Mesozoic, and not in the Tertiary Period.

Part I. New Evidence on the Origin of the Lepidoptera

Recent discoveries of new familial representatives of the homoneurous Lepidoptera by Common (1973) in Australia, by Kristensen (1978) in Brazil, and added information about the Neopseustidae by Davis (1975), has prompted reconsideration of the origin of elements of the Lepidoptera stem.

New evidence suggests that between the end of the Permian and the Jurassic differentiation of early branches of the Lepidoptera stem and their separation from the Mecopteroid stem may have occurred. This necessitates further discussion of the Triassic fossil described as *Eoses triassica* Tindale (1945: 39). When published it was considered an ancestor leading toward the homoneurous branch of the Lepidop-

tera and was placed in a separate suborder, the Eoneura. This view has been rejected by some researchers. Thus Riek (1955), who subscribed to a view that the Lepidoptera only became separate relatively recently, said that consideration of an early Mesozoic appearance would be premature. He said of *Eoses* that it would be difficult to maintain it as a primitive lepidopteran although it conceivably might be ancestral to that order.

New discoveries have encouraged consideration of an earlier Mesozoic origin. Finding of early Cretaceous moths close to *Sabatinca* in amber from Lebanon (Whalley, 1977) and of Eocene Papilionoidea relatively close to the living *Baronia*, by Durden and Rose (1978), has strengthened the view of an earlier Mesozoic origin of the Lepidoptera stem.

After attempting to place *Eoses* correctly, a further pair of wings from the same Mount Crosby Mid-Triassic bed will be described. This fossil suggests differentiation of the Lepidoptera had already begun at that time, especially in forms classified by venational characters as Homoneura.

Dodds (1949: 3) confirmed that the Insect horizon of the Mt. Crosby bed under consideration is beside the track between Portion 92 and Portion 172, Parish of Chuwar, in Queensland. In the view of findings of Jones and de Jersey (1947) the bed lies at the top of the Mid-Triassic. I worked in the bed at various times between 1942 and 1944.

Historical and Taxonomic Review

Preliminary discussion on the taxonomy of *Eoses triassica* is in order. Riek (1955: 661) suggested that the generic name *Eoses* was a *nomen nudum*. He failed to notice that in the original paper the genus was described in the same terms as the species. There was a description and a direct discussion on the likely position of *Eoses* in the development of the Lepidoptera stem. Riek further considered it to be a direct synonym of the Upper Triassic *Mesochorista proavita* Tillyard (1916: Pl. 2, Fig. 2), an insect to which it has some resemblance, but which belongs in the Mecoptera. Of *M. proavita* he says that, save for differing structural details of the vein Sc it could be placed, almost, in the Recent genus *Chorista* Klug (Mecoptera, family Choristidae). Fig. 1 in this paper is based on Tillyard's original figure.

When comparisons are made in detail between *Eoses triassica* and *Mesochorista proavita* there are significant differences:

a) In the forewing the hm vein is present in *Eoses* and extends along the costa; it is not in the *Mesochorista*.

b) The ir vein is present in *Eoses* between R_3 and R_4, but it is absent in *Mesochorista*.
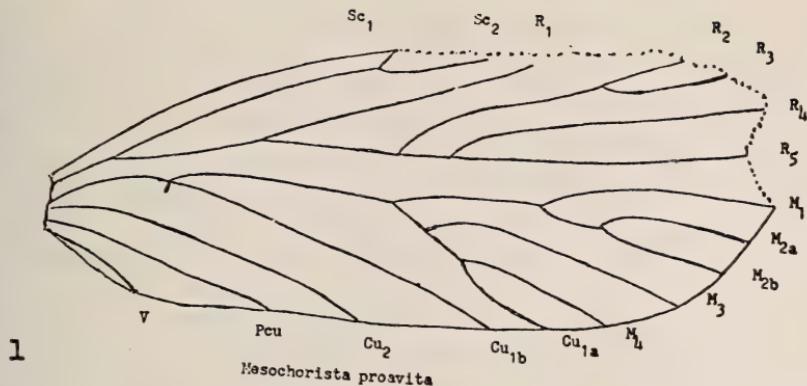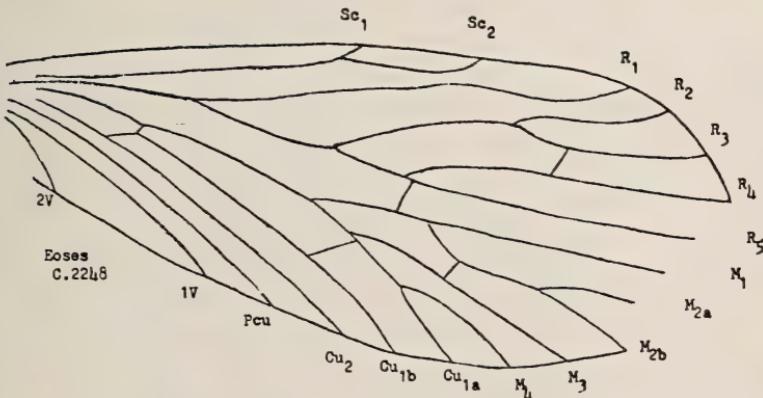
Figs. 1–2. Upper, *Mesochorista proavita* Tillyard, 1916, Upper Triassic (after Till-yard); Lower, Specimen C.2248, Middle Triassic, *Eoses* identified as *M. proavita* Riek (nec Tillyard), after Riek.

c) The rm vein is present in *Eoses*, but not in *Mesochorista*.
d) The im vein is present in *Eoses*, but not in *Mesochorista*.
e) Cu_{1a}/Cu_{1b} fork is present in *Eoses*, but is not in *Mesochorista*.

Some of the above differences may be, in part, due to the difficulties of observing the fossils but I question their being the same. When drawn to similar scales, by taking the distance from the fork of R_1 and R_s to the fork of M_1 and M_2 as base, the wings also are different in form. Finally, they are from very different horizons in the Triassic.

In the Australian Museum collection in Sydney, Riek found a linked pair of wings, their specimen F.39230, which he was able to match
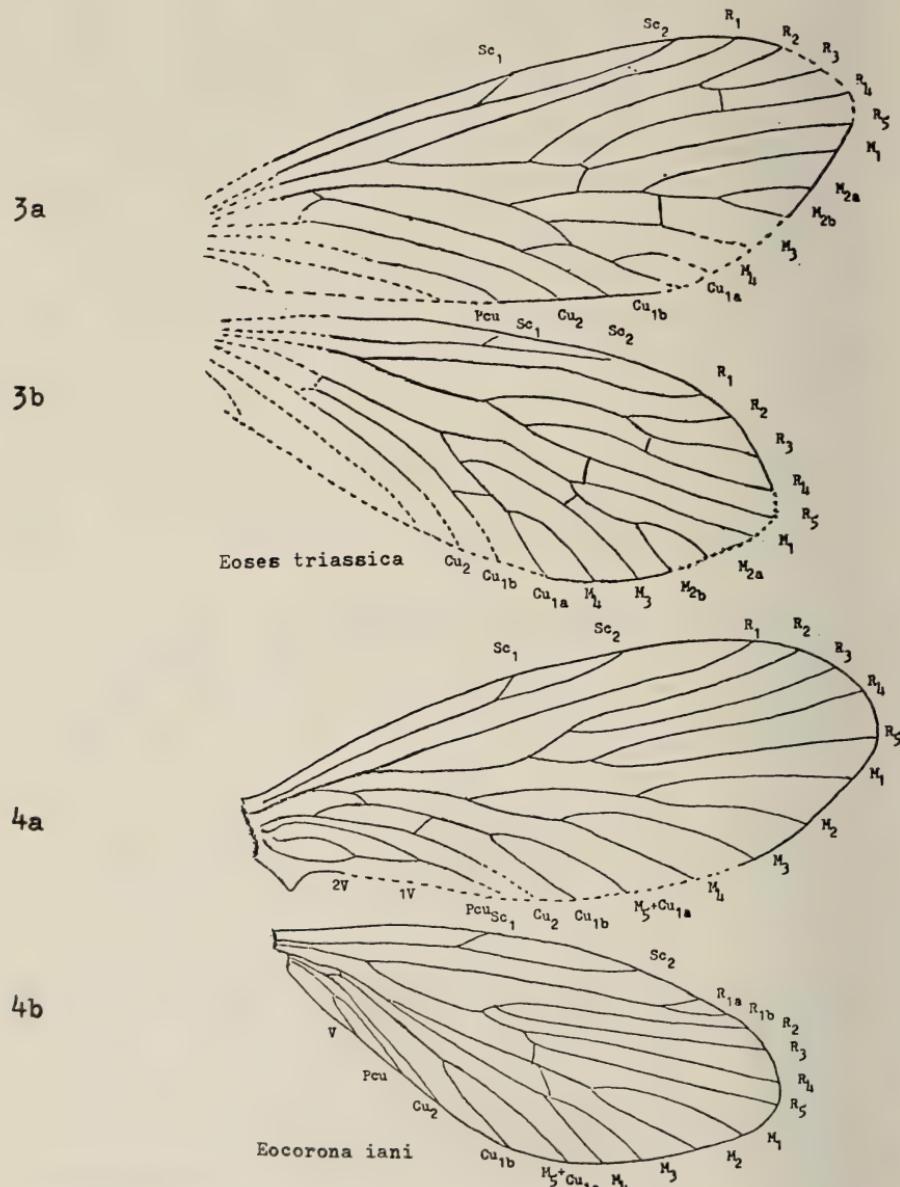
FIGS. 3–4. **3a,** *Eoses triassica* Tindale, 1945, original specimen, F.7853, with data from C.2248 superimposed in dotted line. **3b,** paratype specimen F.7855 with additions suggested in dotted line. **4a,** *Eocorona iani* gen. et sp. nov. Mid-Triassic, Site A, Mount Crosby, Queensland, holotype. **4b,** the same, paratype, identified as a hindwing, from same horizon as holotype.

with the type specimen of *Mesochorista proavita* Tillyard, thus confirming that it was a forewing. Therefore, it appears safe to accept the view that it is the forewings that are being compared between *Eoses* and *Mesochorista*. Unfortunately Riek did not figure the hindwing of this pair. He also obtained a further specimen, C.2248, from the Mount Crosby bed. This he believed to be a *Mesochorista* and thus equated it with *Eoses*. He did figure the new find. It shows similar differences from *M. proavita* as outlined above and definitely is not *M. proavita*.

Specimen C.2248 is smaller than the type forewing of *Eoses triassica*, necessitating an adjustment of the order of 8.7 as against 11.0 to obtain any close match of comparable parts of the venational pattern. Conceding all the imperfections claimed by Riek, as present in the specimen F.7853, a composite drawing affords some substantiation, but suggests that there is less of an apical wing point than suggested in the original interpretation. Figure 3a incorporates in dotted outline additional information suggested by C.2248.

According to Riek the paratype specimen of *Eoses triassica*, F. 7855, is not a hindwing as described, but another forewing, despite its different size and shape. Parenthetically, in the original published drawings of *Eoses* a printer's error in the reduction of the figures made the hindwing proportionally far too large. This is apparent when the published dimensions are noted. It is smaller than the supposed forewing and matches C.2248 in size. I believe that they both are hindwings. When they are directly superimposed there is little need for adjustment and there is considerable correspondence even in small details. The result is shown in Fig. 3b.

Accepting a view that we have present matched fore- and hindwings of a single species, known as *Eoses triassica*, consideration must be given to the specimen C.1595 of Riek (1955: 658, Fig. 5) which he regards as a hindwing. This specimen differs in wing pattern and it is too small to be an actual hindwing of the species under discussion. It seems safe to dismiss it from further consideration as part of the immediate problem. Thus, in my opinion, we have strong indications of the existence of an early member of the Lepidoptera stem, and I believe that Riek has incorrectly synonymized its name with that of a species, *Mesochorista proavita* which belongs in a different order of mecopteroid insects, a group from which it is removed both by structure and by time. The three wings of *Eoses triassica* now known provide us with a useful picture of a Mid-Triassic, and very early lepidopteran.

As summarized by Razowski (1974: 7), the position of *Eoses* has generated several divergent points of view. The finding of the addi-
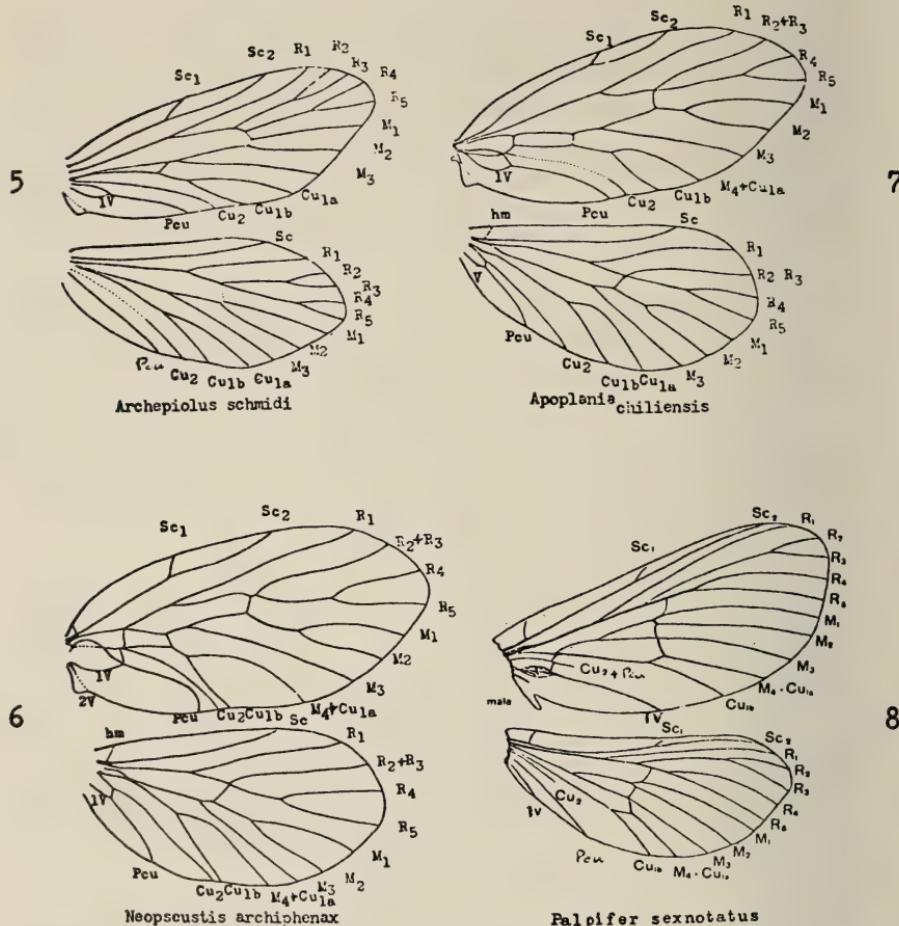
FIGS. 5–8. Upper left, *Archepiolus schmidi* Matuura, 1971, Assam (after Davis, 1975) with altered vein designations. Lower left, *Neopseustis archiphenax* Meyrick, 1928, Burma, China (after Davis: vein designations added). Upper right, *Apoplania chiliensis* Davis, 1975, Chile (after Davis; vein designations added). Lower right, *Palpifer sexnotatus* Moore, 1879, Sikkim (Hepialidae).

tional material by Riek (his specimen C.2248) eliminates the Bourgogne (1951) view that *Eoses* was a pathological specimen. Hennig (1969) followed Riek (1955) in considering it a mecopteran, a position disputed in this paper. The supposed similarities to the Diptera seem specious if both fore- and hindwings are accepted as present. It seems that these authors thought that the Lepidoptera originated at a very late date, implied although not stated, as Tertiary time. The presence of a relatively advanced homoneuran from the Lower Cretaceous im-

TABLE 1. Two estimates of the geological time scale. Age in millions of years before present.

Eras	Periods	Epochs	First estimate	Second estimate
		Recent	0.01	0.015
	Quaternary	Pleistocene	3	1
		Pliocene	6	11
		Miocene	23	25
		Oligocene	35	40
		Eocene	55	60
Cenozoic	Tertiary	Paleocene	65	70
		Cretaceous	135	130
		Jurassic	200	180
Mesozoic		Triassic	210	225
Paleozoic		Permian	235	270

plies earlier development must have occurred in the Jurassic, thus pointing to at least a Triassic base for the order. The inferences of Jeannel (1949) that early Lepidoptera were inhabitants of Gondwanaland in the earliest Mesozoic, and that lines leading to the Cossidae and to the Castniidae were already represented in the Jurassic, are likely to be true.

Time Scale in the Development of the Lepidoptera

A frequent question is how much time has elapsed since the Lepidoptera first appeared. Geologists are not yet in agreement as to time scale, but an origin of the stem in the Triassic would take us back more than 210 million years.

Radiometric records by Banks (1973: 669) suggest the Permian–Triassic boundary at about 235 million years before present, with the Triassic–Jurassic changeover near the 200 million mark. Whalley (1977) in reporting the *Sabatinca*-like species from amber, in Lebanon, of Early Cretaceous date, allowed "at least 100 million years," and quoted another assessment of "an absolute age of 130 million years before the Present." Table 1 is based principally on Banks.

I will now discuss another species from the Mid-Triassic of Mount Crosby, Queensland, which may qualify for recognition as an early member of the Order Lepidoptera.

Wing Impressions from the Mount Crosby Insect Bed

Order Lepidoptera
Family **Eocoronidae** nov.

This family is erected to contain the monotypic species and genus described below. It is from an upper level in the Mid-Triassic of Mt.

Crosby, Queensland. The looped vannal veins of the forewing differentiate this taxon from what is considered to be its nearest known relative, *Eoses triassica* Tindale, 1945, which belongs in a separate family, the Eosetidae, present in the same Triassic horizon. Descriptions of the family, genus, and species are combined below, and are followed by a discussion on its relationships with other early fossil Lepidoptera.

Eocorona Tindale, new genus

Description. Forewing moderately broad, margins well rounded, with rather rounded apical area at about R_5. Costa with Sc_1 and Sc_2 present; R_1 and R_s parting at one-quarter. Second radial fork near one-half, thereafter both tertiary forks are short-stalked and evenly parting. Presence of rm crossvein suspected but not clearly shown in the primary type specimen. Median fork near base, second fork well before middle, thereafter both veins long stalked. $M_1 + M_2$ stalk twice as long as $M_3 + M_4$. M_5 joining Cu near one-third, separating again before the margin. Cubital fork well defined, intercubital crossvein present. Cu_2 extending strongly towards hind margin so far as preserved in the specimen under consideration. Pcu a strong vein running towards margin parallel to Cu_2. Veins 1V and 2V in anal area looping up to join with Pcu well before margin. A broad jugal lobe present.

Type. *Eocorona iani.* From the Mid-Triassic of Mount Crosby, Queensland. The single species so far recognized in this genus appears to be a member of the Suborder Eoneura of the Lepidoptera, as envisaged by Tindale (1945), but its position is subject to revision when more is known of its relationships. A broader discussion of its status and relationship with *Eoses triassica* and other Lepidoptera is given later in this paper.

Eocorona iani Tindale, new species

Description. Characters as set out in the above generic description. Virtually the whole of a forewing discovered, with well formed jugal lobe present. Margins of the wing are clearly evident except between the basal fourth of the hind margin and just below M_3 but the hindmarginal form is approximately defined by the apparent distal terminations of M_5 and Cu_1. The length of the preserved portion of the wing, as shown in Fig. 4a is 8 mm.

Types. Holotype specimens from Site A at Mount Crosby, Mid-Triassic. Type to be deposited in the University of Queensland Geographical Museum as no. C.2327.

Remarks. A second specimen from the same horizon tentatively is considered to be a hindwing of the same species. It also is to be deposited in the same collection as no. C.2331. Its preserved length is 7 mm. This second specimen shares significant features with the designated type specimen. Such differences as exist, indicated in Fig. 4b, suggest the hindwing of an early lepidopteran. It differs in the presence of a small apical fork of R_1. The rm crossvein, uncertain in the type, is well defined, as is also an oblique im vein. Pcu extends to margin and only one vannal vein is present.[1]

First drawings of the above *Eocorona* fossils were made in 1943, but set aside. Interest in them was renewed after the discovery of three species of living Lophocoronidae by Common (1973). There were indications pointing to the Triassic as a probable time for the divergence of the Lepidoptera stem from other mecopteroids. I suggested this in 1945, but the view had been rejected by Riek (1955). As a result of

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[1] Venational designations employed in this paper have been used by this author in many papers on the homoneurous moths of the family Hepialidae and were outlined in Tindale (1941). Due consideration was given then to the recommendations of Snodgrass (1935) about the postcubital (Pcu) and the vannal (V) veins in the anal area of the wing.

developments outlined in earlier paragraphs of this paper regarding *Eoses,* the new evidence afforded by *Eocorona* supports the view that by Triassic times some of the trends in development of the whole homoneurous stem of the Lepidoptera were foreshadowed. Thus it seemed proper to look even before the Mid-Triassic for the actual separation of the two orders Lepidoptera and Mecoptera.

In considering *Eocorona* with *Eoses* as ancestral Lepidoptera, some differences can be found. In the forewings of living Hepialidae, for example, there are only three main M branches with a fourth uniting with Cu_1 near the base of the wing, as was first noted by Tillyard. In *Eocorona* seemingly there is an additional M vein extending to the margin while it is a fifth one which links with Cu near the base (Figs. 4a and 4b). I have an alternative suggestion that M_3 has a bifurcation near the termen in which case there is no M_5. I intend to publish this alternative view in a separate paper. The present interpretation serves to draw attention to some resemblances here and also in the looped vannal veins of the forewing, suggesting a possible link with the Permian *Microptysma* of Martynova (1959). Perhaps the venational characters which lead toward the Lepidoptera were already apparent at the very beginning of the Mesozoic.

In the looping up of the vannal veins of the forewing, *Eocorona* resembles both *Agathiphaga,* and to a lesser extent *Lophocorona.* Dr. I. F. B. Common (personal communication) noted that *Agathiphaga queenslandensis* possesses an M_4 much as in *Eocorona* and suggested that because of both this feature, and the indication that the apex of the wing comes between R_4 and R_5, a link with the Agathiphagidae rather than with the Lophocoronidae might be favored. However he agreed that we are dealing with very primitive lepidopteran characters and these indications do not imply, necessarily, any close relationship. In the absence of parts other than the wings it is not possible, at present, to relate these fossils too closely to any existing family, or to modern classifications based on the structures of other body parts. Indications, based on their homoneurous venations, are that, if the wings are truly matched, they should be considered near ancestors to lines leading to the Dacnonypha of Hinton (1946) and the Monotrysia of Börner (1925), if these divisions have validity.

In comparing *Eocorona* with *Lophocorona,* while keeping *Eoses* in mind, it seems that in the Triassic there were vein modifications which have persisted up to the present day. Some important venational characteristics of present-day Homoneura were already established by that time.

Comparison of *Eocorona* with *Agathiphaga* yields interesting indications of a distant relationship, and also of some major differences. The long fork of R_4+R_5 in *Eocorona* seems to be a major difference, but the condition appears in living hepialids such as *Palpifer* (Fig. 8). In *Eocorona* also, the stalk of R_2+R_3 happens to be short and thus to differ from the length in other Homoneura, but this character is long in *Eoses* and so is comparable with the length in other hepialid genera (e.g., see *Fraus* and *Pharmacis,* and the same condition is seen in *Agathiphaga*). In *Archepiolus* (Fig. 5), which Mutuura (1971: 1133) considers to be the most primitive known of living Dacnonypha, there is a symmetrical branching of the R veins, as in *Eocorona*; the difference is that the stalk portions are longer than the forked ones. Davis (1975) did not comment on this feature when he linked *Archepiolus* with *Neopseustis* (Fig. 6) and with *Apoplania* (Fig. 7), in which there seems to be a specialization linked with some form of scent gland such as appears in the males of *Palpifer sexnotatus* (Fig. 8).

Crampton (1922: 288–229), basing conclusions on available material, suggested that from a pre-mecopteroid array came a line of development leading to Trichoptera and Lepidoptera. He was one of the first to perceive that these two lines paralleled each other very closely and would show common ancestry. Material in the present paper suggests that by Triassic times the early Lepidoptera were already in evidence. Necessity of considering only venational characters limits useful comparisons with other studies (e.g., Kristensen

1975) based on additional anatomical features. However the links he infers between the Lepidoptera, the Trichoptera, and the mecopteroid stem are not contradicted.

Part II. Origin of the Butterfly Stem

The origin of the Rhopalocera, today sometimes called the Papilionoidea, long has been a matter of doubt. Various studies have led to widely different conclusions. This group seems to be directly related to the heteroneurous Lepidoptera, but if their primitive forms have arisen from within that section of the Lepidoptera, their ancestors have yet to be determined to everyone's satisfaction.

The butterflies have been thought to be related to early Geometroidea. They seem, to some, closer to the Butterfly-moths of the superfamily Castnioidea, a group of day-flying species possessing, like them, clubbed antennae and bedecked in gay colors. Their roots can be suggested as linked with the Cossoidea, which, like them are concealed feeders in the larval stages. Other possible origins have been proposed. It is not the purpose of this paper to discuss the full history of such studies. Rather, I consider a small section of the entire problem, based on wing venations and the tracheal systems, as seen in pupae on the day of change into that resting stage, and during the development of the pharate adult.

Much of our knowledge of the origin of the mecopteroid orders of the Insecta has been deduced, of necessity, from the study of fossil wings, usually detached from other body parts. Sound conclusions make it desirable that all structures be given consideration, but wing veins have always received major attention and it may be of some value to look closely at evidence relating to their development in living forms, and to pay particular attention to the tracheae during the first hours after the change to the pupal state, while the tissues are still translucent.

Some work was done on first day tracheal systems in several species of butterflies in Brisbane, Queensland, between 1942 and 1944 and notes were discussed with Dr. F. E. Zeuner, in London, in June of 1944, in light of his then newly published paper (Zeuner, 1943).

Tracheal systems of the developing wings of several typical members of superfamilies of Rhopalocera are shown in Figs. 9–17. On them the tracheae are labelled so that, in general, only discussion of particular points are necessary.

Wing Tracheae in Pupae

In the superfamily Hesperioidea tracheal patterns perhaps retain the greatest number of primitive characters. As represented by the Australian Regent Skipper, *Euschemon*
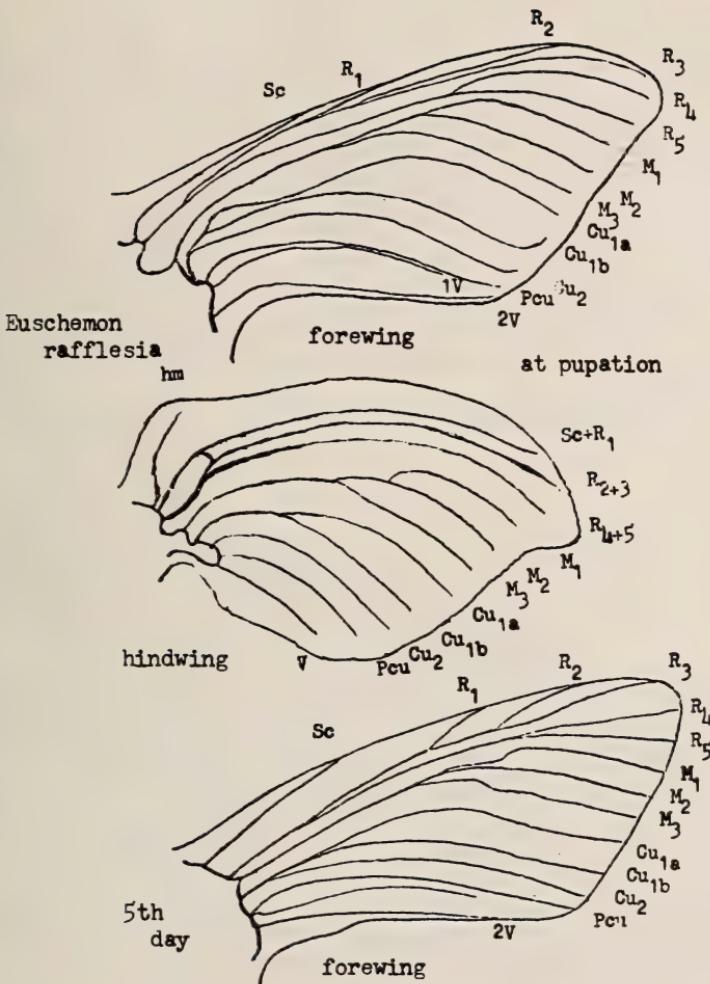
FIG. 9. *Euschemon rafflesia* (W. S. Macleay) 1826. **9a & b,** fore- and hindwing showing tracheal patterns, in life, of newly formed pupa. **9c,** forewing with pupal tracheation on fifth day of pupation.

r. rafflesia (W. S. Macleay) 1826 (Fig. 9a, b), the newly formed pupa, examined at the moment of pupal ecdysis displays a three-branched M series in both wings. In the forewing there are five R vein precursors present; R_2 and R_3 are combined for part of their lengths as a stem separate from that uniting R_4 and R_5, the junction between these two stems being near the base of the developing wing. In the vannal area Pcu and 1V show close approximation towards the wing margin; 2V is present as a strong trachea.

As is characteristic of all heteroneurous Lepidoptera, in the hindwing, the number of R vein precursors is reduced, but there are some hitherto unexplained features in the radial system of *Euschemon*. Hindwing tracheae Sc and R_1 are conjoined almost from their base. This may be the indication of an early specialization in *Euschemon*. A more primitive condition with Sc and R_1 stems separate is seen in the Pierioidea. In
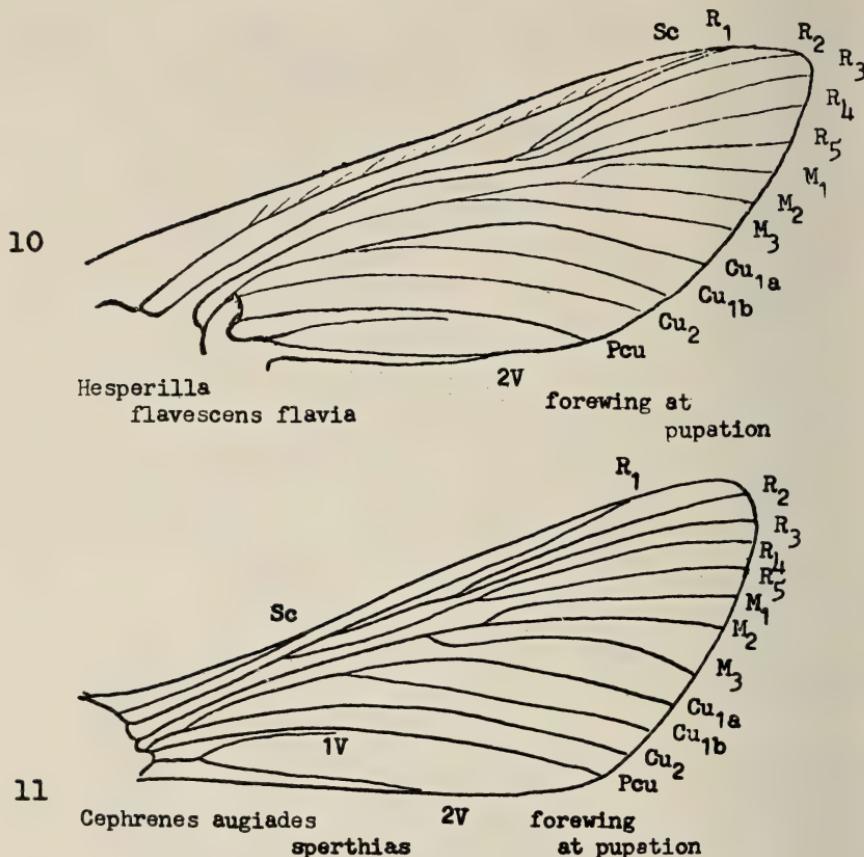
FIGS. 10–11. Upper, *Hesperilla flavescens flavia* Waterhouse, 1941, showing tracheation of forewing on first day of pupation. Lower, *Cephrenes augiades sperthias* (Felder), 1862, with forewing tracheation at pupation.

the newly formed hindwing of *Euschemon* R_2+R_3 and R_4+R_5 seem thus to be represented by separate tracheae. This is a revised interpretation since, according to Tillyard (1919), and to earlier writers on venation, Sc has been considered to be present as a separate trachea or vein, the others present being considered to be respectively R_1 and R_s. The significance of this revision will be suggested in a later paragraph, after other wings have been discussed. In the hindwing only two post-cubital tracheae are evident, since either 1V, or less likely Pcu has become obsolete, while 2V is present as a strong trachea.

In *Euschemon*, on the fifth day of pupation (Fig. 9c), the hindwing details are obscured, but those of the forewing are still clear. The reduction of 1V of the forewing is now marked, and that of 2V also has begun. This is a condition in more evolved Hesperioids, as illustrated in the first day pupae of *Hesperilla flavescens flavia* Waterhouse, 1941 (Fig. 11), and *Cephrenes augiades sperthias* (Felder), 1862 (Fig. 12). There is a considerable difference in the relative lengths of the Sc trachea in these three species.
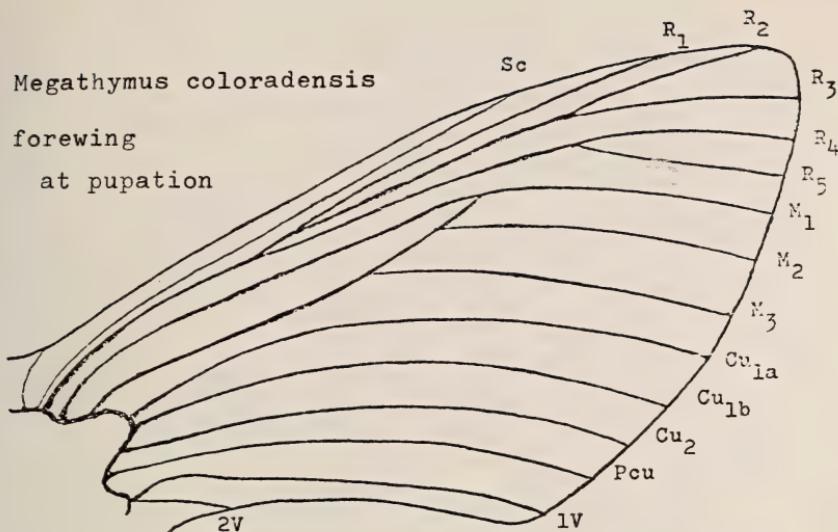
FIG. 12. *Megathymus coloradensis* Riley. Forewing tracheation, in life, on day of pupation.

Through the help of Mr. Ron S. Wielgus I examined first day pupae of *Megathymus coloradensis navajo* Skinner from Maricopa Co., Arizona. As shown in Fig. 12 there are resemblances to *Euschemon* in features of the forewing, as examined within the first four hours of pupal ecdysis. Trachea Cu_{1a} is separate from M from the base. However in one specimen it had already become approximated to M from the base to about one-third of its length, suggesting a change of direction as development proceeded. The full expression of the tracheae in the anal portion of the wing indicates a lesser degree of specialization than in any other butterfly family.

The Papilionoidea, as represented by newly formed pupae of the Orchard Butterfly, *Papilio aegeus aegeus* Donovan, 1805, from Mount Tamborine, Queensland (Fig. 13) show some primitive features in the tracheal system. The fork between R_2+R_3 and R_4+R_5 in the forewing is similar to that in *Euschemon* and occurs well down toward the base of the wing, while the second forking at which these vein precursors separate lies near the middle of the developing wing. This may be a very old feature. The forewing shows Cu_2 as a separate trunk, while Pcu is a strong trachea. Reduction of 1V and 2V has occurred and 1V does not reach wing margin.

In the hindwing of *Papilio aegeus* hm trachea is lost, a definite absence as compared with the condition in the Hesperioidea where it is a strong trachea. Sc, R_1 and R_s are united in a single basal stem and R_s appears to be a single branch; signs are present of a fourth M; this disappears near the middle of the wing. All three cubital tracheae arise from a common stem and only two post-cubital tracheae are in evidence; these are considered to be respectively Pcu and 1V. It is likely that in *Papilio aegeus* adults, 2V is lost, as foreshadowed here in the pupal wing.

In the Common Australian Bean Blue, *Zizina otis labradus* (Godart), 1819, shown in Fig. 14 representing the Riodinoidea, the forewing of the first day pupa shows the same split, back between the stems (R_2+R_3) and (R_4+R_5), that is evident in the Papilionoidea and the Hesperioidea. The R_5 trachea is well developed in the midwing area, but loops down to touch M_1 before turning away again to run parallel to R_4. Near the margin it fades into minute branchlets. The apparent migration of M_1 to a position on the R stem in the adult wing thus is foreshadowed, and the position of the vein M_1
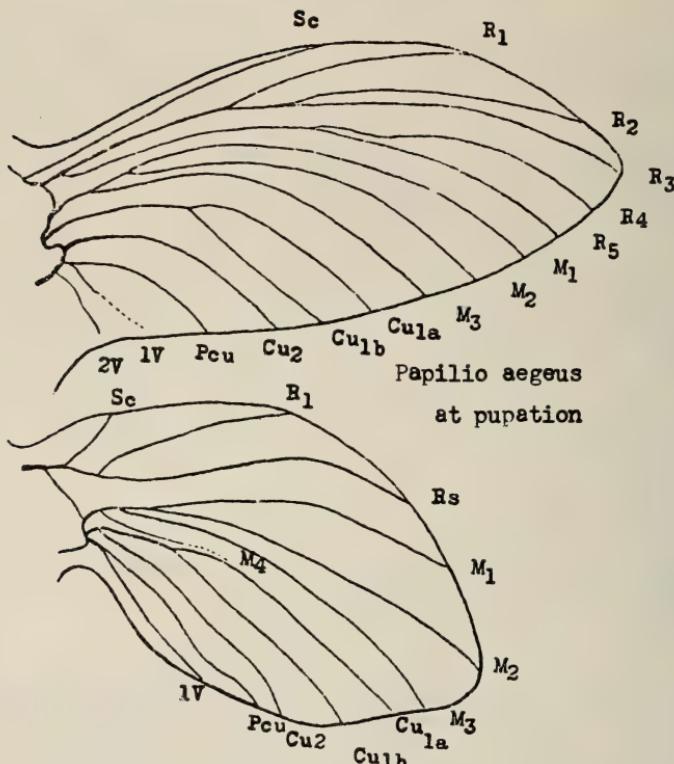
FIG. 13.   *Papilo aegeus* Donovan, 1805. Wing tracheation, in life, in newly formed pupa.

usually high up on the R_4+R_5 stem is explained by the day-old pupal condition. Another seeming specialization of the radial venation of the lycaenid adult, apparent in the early pupal tracheation, is the fusion of Sc and R_1 which is usual in the adult. An additional complication appears later in pupal life with the junction of the combined $Sc+R_1$ usually shown as R_1, and R_2. In Australian species the independent condition of R_1 and R_2 is seen in *Candalides*, while progressive union may be traced through adults of *Nacaduba*, where R_1 and R_2 touch and then separate again, to *Theclinesthes* in which fusion is continued to the wing margin.

All the cubital and vannal tracheae are present in the early *Zizina* pupa, but Cu_2 sometimes does not reach the wing margin and shows signs of weakening, while 2V is hard to see and seemingly is on the way to disappearing. Thus it seems clear that Cu_2 is the vein that disappears in the adult wing, while Pcu remains as a strong vein and vannal veins are wanting. The pupal hindwing has not been studied in *Zizina*.

In the Pierioidea as represented by the Lemon Migrant, *Catopsilia pomona pomona* (Fabricius), 1775, the tracheation of the newly formed pupa, as shown in Fig. 15, shows some very primitive characters, along with some marked specializations. In the fore-wing the R tracheae are as in *Papilio*, as also Sc. Only two, instead of three M tracheae are present. As first demonstrated by Zeuner (1943), probably it is M_2 which has dis-appeared. However in *Dismorphia*, the most primitive of the Pierids, if it is one, M_2 is said to be present. In the advanced pupa of *Catopsilia* it may appear in the forewing,
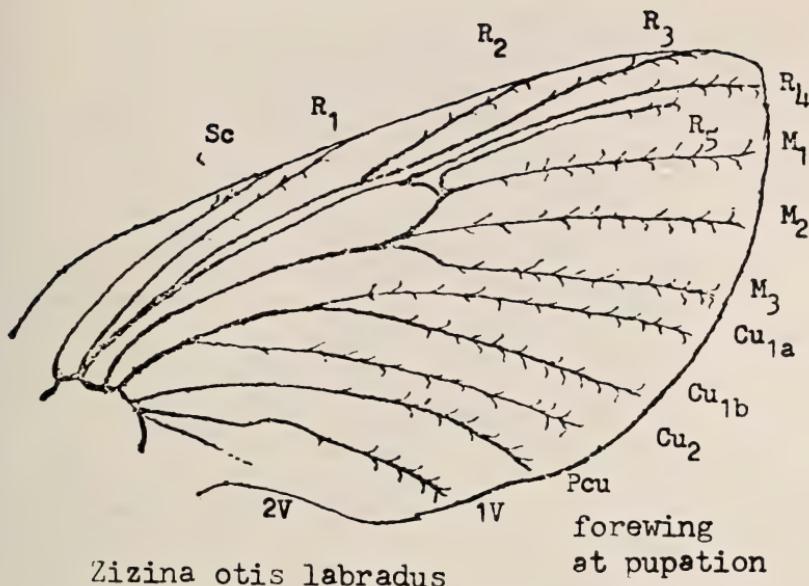
FIG. 14. *Zizina otis labradus* (Godart), 1819. Forewing tracheation on first day of pupation.

but not in the hindwing, and it fails to appear as a vein in the adult butterfly through a complex union with R.

In the hindwing of the newly formed *Catopsilia* pupa hm is a strong trachea which disappears later. R tracheae apparently show a primitive condition where R_1 is present and R_s is a two-branched trachea. Both $R_2 + R_3$ and $R_4 + R_5$ are present, as in the early pupa of *Euschemon*. This condition persists into the late pupal stage. Cu_2 has its origin near the base of the wing as in the first day *Euschemon* pupa. Pcu is a strong trachea as in the forewing, and there is only a single vannal trachea; in the forewing it seems to be 1V which is present while 2V is vestigial or absent; however the reverse may be the case in the hindwing. In the advanced pupa M_2 does appear in the forewing but not in the hindwing; in the latter a vestigial 1V is seen, but it does not reach the margin of the wing. Presence of these late tracheae help in determining the identification of the veins which have dropped out in the adult hindwing. The hm trachea of the first day pupa seems to disappear in a later stage.

In the Danaioidea, generally considered the most specialized of the superfamilies of the butterflies, as represented here by the Crow Butterfly, *Euploea core corinna* (W. S. Macleay), 1826, the fine branchlets of the first day tracheae are very well evident, as they are also in *Zizina*. As shown in Fig. 17 the R region is closely compressed along the costa; there is the same deep schism separating $R_2 + R_3$ from $R_4 + R_5$ as in all the other superfamilies so far considered. In the forewing also there is a midwing branching of M_3 which runs obliquely down to join Cu_{1a} before the middle, as if it were a vestige of an M_4 such as is found in archaic Lepidoptera. Cu_2 originates close to the base of the common Cu stem. Three post-cubital tracheae appear to be present, but 1V appears to be vestigial.

In the hindwing of the first day *Euploea* pupa hm is present, R_s is a simple trachea, Cu_2 is from the very base of the common stem and Pcu is a mere vestige, while both 1V and 2V are strongly developed. Differences between the Pierioidea and the Dana-
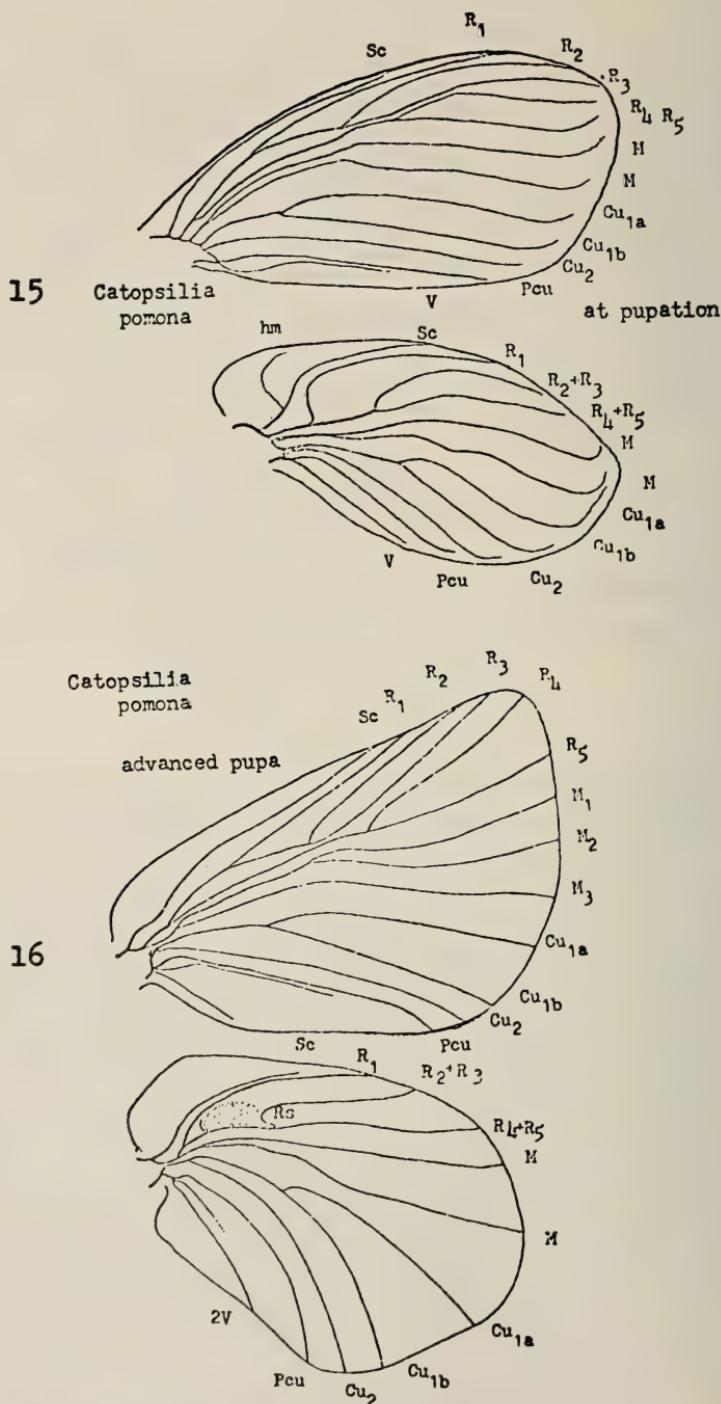
FIGS. 15–16. *Catopsilia pomona* (Fabricius), 1775. Upper, wings showing trachea-
tion on first day of pupation. Lower, the same showing tracheae at a late stage of pupal
life.
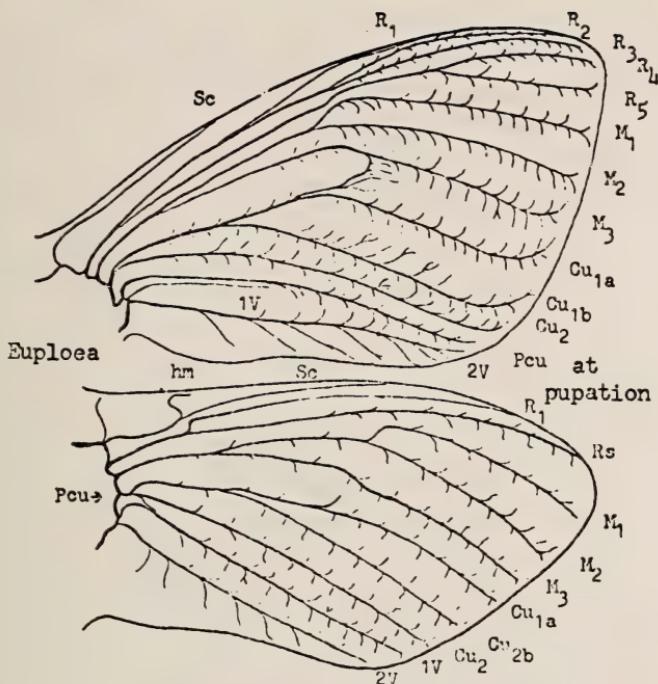
FIG. 17. *Euploea core corinna* (W. S. Macleay), 1826. Wings showing tracheae in life on first day of pupation.

ioidea in the vannal region of their developing wings suggest that in their common ancestor Pcu and both vannal veins were well developed. As is indicated in the discussion there may be another interpretation for the radial region of the hindwing as described in the above text and marked on Fig. 17.

An Archetype for the Butterflies

Bearing in mind the data derived from study of the tracheal systems and the rich information provided by Zeuner (1943) and his many predecessors I have taken what seem to me the most primitive characters displayed in each of the superfamilies and developed a possible archetype for the butterflies. It appears as a frenate lepidopteran with a venational pattern approximating that shown in Fig. 18.

No known lepidopteran possesses all the characters indicated in this reconstruction. If the concept bears resemblance to reality the butterflies must be considered a very archaic group with roots going back to the beginning of the development of the heteroneurous Lepidoptera, as distinct from the homoneurous ones.

Of living families of moths the concept seems suggestive of the Castnioidea, but may also bear comparison with the Cossoidea. It seems unlikely to be very directly linked with such advanced super-
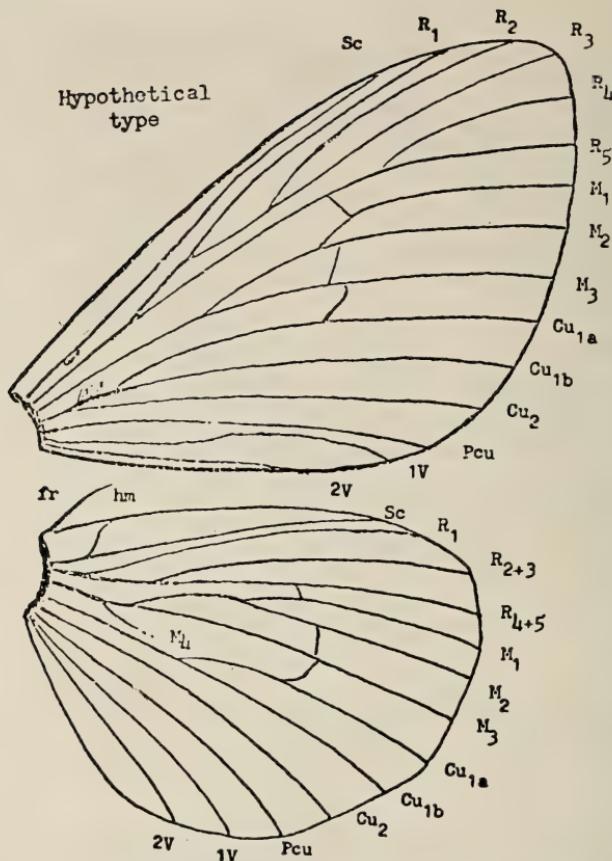
FIG. 18.   Hypothetical archetype of the Rhopalocera or Butterflies.

families as the Geometroidea. Tillyard (1926: 455) sought a common ancestor near the Pyraloidea and the degraded Pterophoroidea. The presence of pilifers on the pupae of the butterflies, a character they share with the two above mentioned groups may suggest a link but the connections must be relatively remote. The most primitive of the Pyraloids seem to show some resemblances in the forewings but their hindwings are sufficiently different to suggest relationship only far down on the Lepidoptera stem.

The survival of a frenulum in the hesperioid *Euschemon* as well as its presence in the main line of the more primitive groups of the heteroneurous moths indicates a common frenate ancestor. This common ancestor must have possessed five main radial veins in its forewing. In the hindwing there was a reduction from a primary five to

a lesser number of radial veins. It has long been considered that all heteroneurous Lepidoptera possessed only two R veins in the hindwing, a clear dichotomy. However the attempt to explain the tracheal and venational patterns of *Catopsilia* and *Euschemon* has led to the conclusion that the ancestral butterfly may have retained three of the five radial veins in its hindwing instead of the two generally recognized as present in the heteroneurous moths. If this interpretation yields a true picture of the ancestor it would suggest the possibility of a fundamental separation somewhat greater than hitherto has been envisaged.

Accepting the idea of an ancestrally divided R_s, and combining it with the fact that the early pupal stages of the butterflies show a deeply divided (or split) condition in the forewing, separating the stem of R_2+R_3 from that of R_4+R_5, we can conceive the condition as very archaic. Zeuner (1943: 300) had noticed this splitting back of the radials in this fashion as occurring in some heteroneurous families of the moths. At any rate this trait does not appear to be a character of the advanced families.

Perhaps the butterflies have from very early times moved along a different evolutionary path, one unsuspected by Comstock (1918:334). He may have come near the truth when he observed that in the Pieridae another trachea appeared to be attached to R but thought that trachea M in some unexplained manner had been transferred to R; he ascribed the condition to a supposed atrophy of the main stem of the media. His observations were made on the pupal hindwing of the Cabbage White, *Pieris rapae* (Linnaeus), 1758. Zeuner (1943) observed Comstock's error but did not follow up the implications of this fact. So far as the R_s of the hindwing is concerned the pierids are here presumed to have preserved a primitive condition, one common to the whole ancestral line of the butterflies. On the other hand they seem to have become specialized in the reduction of the media to a two-branched condition, a change that does not appear to have affected any other butterfly line. In *Euschemon* R_s can be seen as branched, as in the pierids, but there is a specialization in that R_1 joins with Sc just after the branching of R_s so that the three branched radial condition is less apparent.

In the tracheation of *Papilio* there is room for two different interpretations, in the hindwing, of the relationship between Sc and radials. The usual interpretation has been shown in Fig. 13, but it seems possible, in the light of the conditions prevailing in *Catopsilia* and *Euschemon* that Sc should be considered to be $Sc+R_1$, the trachea labelled as R_1 really is R_2+R_3, and R_s should be regarded as R_4+R_5. This interpretation seems to make the relationship clearer.

When we reexamine the hindwing of *Euploea* as shown in Fig. 17 it becomes easier to accept a similar change in the interpretation of the Sc and R situtation since it is possible that the short trachea labelled as hm is really Sc while R_1 is separate from R_s from the very base of the wing. In support of this interpretation, there is an otherwise unexplained small trachea at the base of the wing which perhaps is the real hm.

Thus it may seem that these limited studies of the early pupal tracheation, of *Euschemon* and *Catopsilia* in particular, may have revealed some vital clues, leading to a possible elucidation of the problem of the origin of the butterflies. Because Tillyard (1919) had to rely only on data provided by an advanced pupa (tenth day) he failed to see the earlier condition in *Euschemon*, which has been so informative. These data lead, in conjunction with data on the first day pupa of pierids to the conclusions set out here.

Fitting the hypothetical prototype (shown in Fig. 18) to present-day butterfly families necessitates taking note of certain lines of specialization. In the forewing these include the following trends:

a) loss of the discoidal portions of the stem of the M veins;
b) the obsolescence of the r-m crossvein by reduction so that M_1 has come to be directly connected to R_5;
c) the reduction of Cu_2 so that it is represented by a basal loop with Pcu;
d) the usual presence of only two, or even only one post-cubital vein, instead of three (usually it is 2V which is absent) although 1V is often present (if only in the basal part of the wing, either looping up to join Pcu, or fading out in the distal part of the wing).

In the hindwing, specializations include the following:

a) coalescence of Sc and R_1 to form a single vein;
b) the union of R_4+R_5 with M_1 with loss of the r-m crossvein;
c) the reduction, but only in the advanced pierids, of the M region by loss of M_2;
d) the disappearance or modification of the r-m crossvein;
e) the obsolescence of at least one post-cubital vein.

The above trends have progressed to different degrees in the superfamilies of the living butterflies. As Durden & Rose (1978) have shown by their discovery of Middle Eocene butterflies of species as far advanced as some living forms, it seems clear that many of the venational trends were determined already by the very beginning of the Tertiary period.
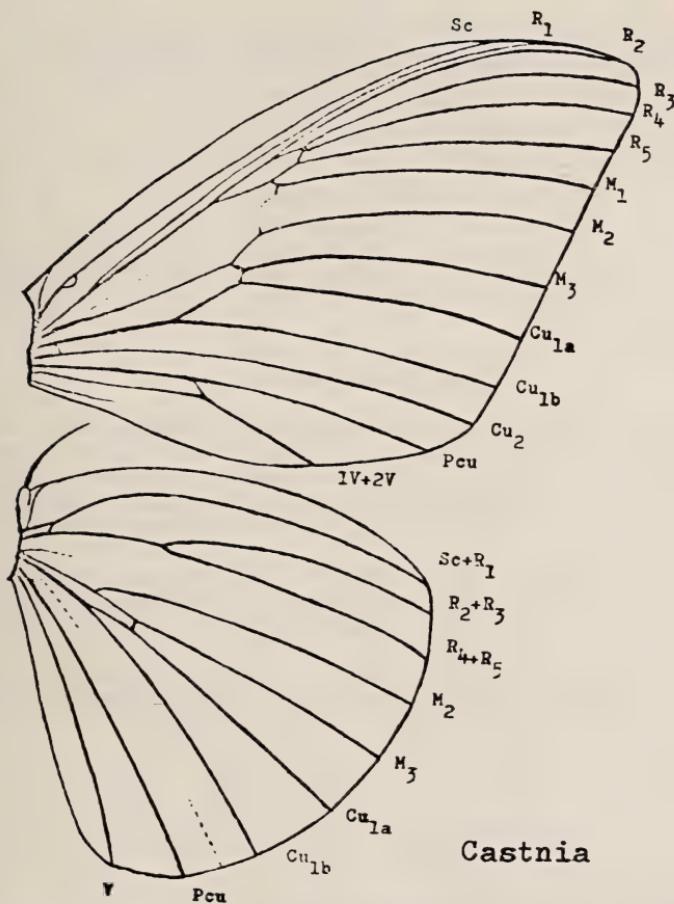
Fig. 19. *Castnia licoides* Boisduval, 1875, from Bolivia, male venation.

The hypothetical archetype drawing bears sufficient resemblance to a member of the Butterfly-moth family Castniidae to suggest a rather closer relationship than had been previously considered. Several venational features support a view that they could have diverged directly from an early common stem.

Fig. 19 depicts the venation of a male Castniid, identified as *Castnia licoides* Boisduval, and taken near Cochabamba, Bolivia, in March 1975. The specimen was kindly given to me by Mr. Sharpe H. Osmundson of San Jose, California. In this *Castnia* the relatively complete venational pattern of the forewing, as theorized for the ancestral butterfly, is of interest. A principal difference is the retention of an ir

crossvein linking R_3 and R_4. This appears to have disappeared from all the butterflies. Study of the Castniidae may enable us to obtain still earlier indications of the development of the butterflies. Study of the first day pupal tracheation of the Castniids is needed and such material is actively sought both in Australia and South America.

In the hindwing of *Castnia* there is a fusion of $Sc+R_1$, the same trend present in the true butterflies. R_2+R_3 and R_4+R_5 are also indicated as forming the radial veins. An apparent specialization is the obsolescence of M_1. Tracheal studies may help in our understanding of this development.

ACKNOWLEDGMENTS

LITERATURE CITED

BANKS, P. O. 1973. Permian-Triassic radiometric time scale. Permian and Triassic systems and their mutual boundary. Ed. A. Logan & L. V. Hills. Calgary, Canad. Soc. Petrol. Eng. pp. 669–677.

BOURGOGNE, J. 1951. Ordre des Lépidopterès *in* P. Grassé: Traité de zoologie. 10: 172–448.

COMMON, I. F. B. 1973. A new family of Dacnonypha (Lepidoptera) based on three new species from Southern Australia, with notes on the Agathiphagidae. J. Aust. Entomol. Soc. 12: 11–23.

———. 1975. Evolution and classification of the Lepidoptera. Annu. Rev. Ent. 20: 183–203.

COMSTOCK. J.H. 1918. The wings of insects. Ithaca, N.Y. 430 pp.

CRAMPTON, G. C. 1922. Notes on the relationships indicated by the venation of the wings of insects. Canad. Ent. 54: 206–216, 222–235.

DAVIS, D. R. 1975. Systematics and zoogeography of the family Neopseustidae with the proposal of a new superfamily (Lepidoptera: Neopseustoidea). Smithsonian Contrib. Zool. 210: 1–45.

DODDS, B. 1949. Mid-Triassic Blattoidea from the Mount Crosby Insect Bed. Univ. of Queensland. Dept. Geol. 3(10): 1–11 (geological notes and sketchmap).

DUMBLETON, L. J. 1952. A new genus of seed-infesting Micropterygid moths. Pac. Sci. 6(1): 17–29. [*Agathiphaga*]

DURDEN, C. J. & ROSE, H. 1978. Butterflies from the Middle Eocene: the earliest occurrence of fossil Papilionoidea (Lepidoptera). The Pearce-Sellards Series. 29: 1–25.

EHRLICH, P. R. 1958. Comparative morphology, phylogeny, and higher classification of the Butterflies (Lepidoptera: Papilionoidea). Univ. Kansas Bull. 39(8): 305–370.

FORBES, W. T. M. 1932. How old are the Lepidoptera. Amer. Natur. 62: 452–460.

HENNIG, H. 1969. Die Stammesgeschichte der Insekten. Frankfurt am Main. pp. 71, 368.

HINTON, H. E. 1958. Phylogeny of the Panorpoid orders. Annu. Rev. Ent. 3: 181–206.

JONES, O. A. & DE JERSEY, N. J. 1947. The flora of the Ipswich Coal Measures—Morphology and floral succession. Pap. Univ. Queensland. Brisbane. n.s. 3(3): 1–70.

KRISTENSEN, N. P. 1975. Phylogeny of hexapod "orders." A critical review of recent accounts. Z. Zool. Syst. Evolutions-forschung 13(1): 1–44.

——— & NEILSEN, E. S. 1979. A new subfamily of micropterigid moths from South America. A contribution to the morphology and phylogeny of the Micropterigidae, with a generic catalogue of the family (Lepidoptera: Zeugloptera). Steenstrupia 5(7): 69–147.

MUTUURA, A. 1971. A new genus of a homoneurous moth and the description of a new species (Lepidoptera: Neopseustidae). Canad. Entom. 103(8): 1129–1136. [Archepiolus p. 1129]

RAZOWSKI, J. 1974. Phylogeny and classification of Lepidoptera. Acta Zool. Cracoviensia. 19(1): 1–20.

RIEK, E. F. 1953. Fossil mecopteroid insects from the Upper Permian of New South Wales. Rec. Australian Mus. 23(2): 55–87.

——— 1955. Fossil insects from the Triassic Beds of Mount Crosby, Queensland. Aust. J. Zool. 3(4): 654–691.

——— 1956. A re-examination of the mecopteroid and orthopteroid Insecta from the Triassic beds at Denmark Hill, Queensland, with descriptions of further specimens. Aust. J. Zool. 4(1): 98–110.

——— 1970. Fossil History. C.S.I.R.O. Insects of Australia. Melbourne. pp. 168–186.

SNODGRASS, R. E. 1935. Principles of insect morphology. New York, McGraw Hill.

TILLYARD, R. J. 1916. Mesozoic and Tertiary insects of Queensland and New South Wales. Queensl. Geol. Survey Pub. 253: 11–47. [Mesochorista proavita p. 30, Pl. 2, Fig. 2]

——— 1919. The panorpoid complex. Part 3: the wing venation. Proc. Linnean Soc. New South Wales 44(3): 533–718.

TINDALE, N. B. 1941. Revision of the Ghost Moths (Lepidoptera:Homoneura, family Hepialidae) Part 4. Rec. S. Australian Mus. 7(1): 15–46.

——— 1942. loc. cit. Part 5. 7(2): 151–168.

——— 1945. Triassic insects of Queensland 1. Eoses, a probable lepidopterous insect from the Triassic Beds of Mt. Crosby, Queensland. Proc. R. Soc. Queensl. 56(5): 37–46.

——— 1963. Origin of the Rhopalocera stem of the Lepidoptera. Proc. XVI Int. Congr. Zool. 1: 304.

——— in press. The origin of the Lepidoptera relative to Australia. in A. Keast, Ed. Ecological Biogeography in Australia. The Hague, Junk.

WHALLEY, P. 1977. Lower Cretaceous Lepidoptera. Nature 266: 526.

——— 1978. New taxa of fossil and Recent Micropterigidae with a discussion of their evolution and a comment on the evolution of Lepidoptera (Insecta). Ann. Transvaal Mus. 31(8): 71–90.

ZEUNER, F. E. 1943. On the venation and tracheation of the lepidopterous fore wing. Ann. Mag. Nat. Hist. 11(10): 289–304.

SOME FACTORS RESPONSIBLE FOR IMBALANCES IN THE AUSTRALIAN FAUNA OF LEPIDOPTERA[1]

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ABSTRACT. Major imbalances in the Australian fauna of Lepidoptera occur in families with high percentages of endemism, e.g., Tortricidae and Eucophoridae, which are associated with typically Australian plant communities and which have evolved especially with *Eucalyptus*. Events affecting the Australian environment from the Tertiary to present are discussed. Utilization of parts and stages of *Eucalyptus* by lepidopterous larvae is described. It is probable that similar selective factors were responsible for extraordinary species radiation in both Australian xerophytic plants and the insects dependent upon them.

The first Lepidoptera are believed to have evolved at least as early as the lower Cretaceous, and by the mid-Cretaceous forms similar to some of the more advanced Lepidoptera were already in existence (MacKay 1970). The greatest development of the Lepidoptera probably accompanied the proliferation of the angiosperms (Common, 1975) during the late Cretaceous epoch, and especially during the Tertiary. Nothing is known of the composition of the Australian lepidopterous fauna of the Tertiary, but it seems probable that it was very different from that of the present day.

The following greatly simplified sequence of events affecting the Australian environment from the Tertiary onwards (Galloway & Kemp, 1979) must have fundamentally influenced the composition and distribution of the Australian flora, and also the composition and distribution of the present-day fauna of Lepidoptera and other insects. From the lower Tertiary to the mid-Miocene the Australian continent was extremely flat, with uniformly poor soils and a relatively uniform moist, warm climate. A mesophytic flora was widespread, including various rain-forest genera such as *Nothofagus,* and typically Australian genera such as *Eucalyptus, Casuarina, Acacia,* and present-day genera of Proteaceae and grasses. Some mountain building occurred in the late Miocene and Pliocene, especially towards the eastern coast, culminating in the Kosciusko uplift, followed by extensive weathering and dissection in the eastern highlands. Marked fluctuations in climate were a feature of the Pliocene, with alternating periods of relatively dry and relatively moist conditions. Rapid changes in climate continued into the Pleistocene, associated with the formation and melting of Antarctic ice. However, glaciation was restrict-

ed to Tasmania and the Kosciusko area. Fluctuations in sea level through a range of some 200 m during this period produced intermittent land connections between the Australian continent and New Guinea in the north and Tasmania in the south. Intermittent favorable corridors connecting the south-east and the south-west of the continent were also created, as well as latitudinal shifts in climatic zones. The establishment of extensive dune systems before the end of the Pleistocene must have also represented significant biological barriers.

Progressive aridity from the late Miocene onwards favored the establishment of a xerophytic vegetation over much of the continent. The major pressures which were imposed on the widespread mesophytic flora of the early Tertiary resulted in the gradual retraction of the less adapted species to refuges along watercourses and in the moister areas of the east and south-east. Fluctuating climatic conditions, and innumerable modifications to the physical nature of the environment, including minor lava flows, weathering, dissection and the deposition of shales, sandstone, limestones, and alluvial soils, led to great habitat diversity. The successive retractions, expansions and migrations of the flora, and the associated fragmentation of populations and isolation of species, resulted in extensive species divergence and evolutionary radiation, and the gradual production of the diverse relatively xerophytic plant communities which occupy so much of Australia today.

Australia is still a relatively flat continent, rising to a maximum altitude of only 2100 m in the south-east. The soils on the whole are poor. An area equal to about one-third of the continent, reaching the coast near the tropic in the west and the Great Australian Bight in the south, has a rainfall of less than 25 cm annually. Beyond this area the rainfall increases in more or less concentric belts towards the coast, but two-thirds of the continent can be classified as semi-arid or arid, and much of the remainder is subject to long dry periods. In contrast, a small area of north-eastern Queensland has a rainfall of 400 cm annually, and the western coast of Tasmania more than 200 cm. The north of the continent receives mainly summer rains, whereas the south receives mainly winter rains.

Very broadly the present-day vegetation of Australia can be divided into the following major categories. In the north-east and in small pockets along the eastern coast, mainly in areas with a rainfall in excess of 150 cm annually, rain forest occurs, tropical in the north, subtropical in southern Queensland and New South Wales. In addition there are patches of temperate rain forest in Victoria and western Tasmania, and fragments of monsoon or gallery forest in northwestern Australia and the Northern Territory. Floristically the northern rain

forests have much in common with those of south-east Asia. Else-
where in Australia where the rainfall exceeds 37.5 cm annually, there
are extensive areas of sclerophyll forests and savannah woodlands,
with *Eucalyptus* species as dominants. Eucalypts do not occur in
rain forest and the few that are found in the arid zone are distributed
along watercourses or in special habitats. In the south, mainly in the
25–37.5 cm winter rainfall belt, mallee eucalypt communities are fre-
quently developed. The arid zone of less than 25 cm rainfall annually
supports various xerophytic plant communities, including extensive
scrubs dominated by mulga and other species of *Acacia*, and grass-
lands containing native grasses and other herbs, but especially por-
cupine grass (*Triodia*).

The Lepidoptera of the Australian rain forests have been derived
mainly from the Oriental and Papuan areas, and share many genera
and species with south-east Asia and New Guinea. The characteristic
Australian elements in the fauna are found in the sclerophyll and arid
plant communities and no doubt have been evolved along with them.
The two plant genera most frequently utilized as food by Australian
Lepidoptera are *Eucalyptus* (Myrtaceae) and *Acacia* (Mimosaceae),
but other genera of Myrtaceae and members of such typically Austra-
lian families as Proteaceae, Casuarinaceae and Epacridaceae (to name
only a few) are frequently used. It is interesting to observe that of the
380 known species of butterflies only four polyphagous species of
Lycaenidae have been recorded feeding on *Eucalyptus*, and relative-
ly few feed on other typically Australian plant genera.

To the casual visitor, and indeed to many Australians, the sclero-
phyll forests appear to be monotonously uniform, dominated as they
are by *Eucalyptus*, often with an understory of shrubs featuring *Aca-
cia*, Proteaceae, Fabaceae, Myrtaceae and Epacridaceae. There cer-
tainly is a similarity about them, but to the more discerning observer
they are far from uniform. There are at least 600 species of *Eucalyptus*
and some 600 species of *Acacia* in Australia. In any restricted area
the distribution of the dominant eucalypt species is controlled by
such factors as soil moisture and soil nutrients, and slight changes in
the microhabitat produce changes in the *Eucalyptus* dominants
(Pryor, 1959). Each community usually has two, but sometimes up to
six, co-dominant eucalypt species growing in stable associations.

Eucalypts range in size from dwarfs only a meter or two in height
to forest giants. Most species are xerophytic and grow in localities
where there is a marked shortage of water for a major part of the year,
either as a summer drought in the winter rainfall areas of the south,
or as a winter and spring drought in the north where the rainfall is
largely confined to the summer months. Most are also resistant to fire

and a few are tolerant of sub-zero temperatures at the treeline in southeastern Australia. Resistance to drought and fire is favored by the exceptionally thick bark of most species, and the development of a lignotuber, a swelling of the trunk at or just below ground level from which dormant buds can produce new shoots after the above ground parts of the tree have been destroyed. A mallee is a form of dwarf eucalypt which has a very large lignotuber below ground level and, instead of a single trunk, the lignotuber produces several branches which appear as a group of small slender trees. There are many species of mallee. Although three or four species of *Eucalyptus* occur in areas north of Australia, including New Guinea and Indonesia, the genus is believed to have originated in Australia.

The genus *Eucalyptus* is attacked by a wide range of Lepidoptera and other insects, and compared with eucalypts planted in many other parts of the world those which grow naturally in Australia are frequently retarded in growth by insect attack. Recurring severe insect defoliation sometimes kills the trees. Larvae of Cossidae, Hepialidae and Xyloryctidae bore in the trunk, bark and roots of eucalypts. Many species in other families mine in or devour the leaves, and a few feed on the flowers or woody seed capsules. Some of the foliage feeders restrict their attention to the young terminal growth, others to the mature leaves, and still others confine their feeding to the juvenile leaves (those leaves produced by the young eucalypt plant which may differ so much from the mature leaves in form and color that they might appear to belong to a different species). Families that include substantial numbers of species dependent on living *Eucalyptus* trees are the Hepialidae, Incurvariidae, Nepticulidae, Cossidae, Oecophoridae, Gelechiidae, Geometridae, Lasiocampidae, Anthelidae and Notodontidae. A few species in other families also feed on *Eucalyptus*, but it is interesting to note that several families such as the Phyllocnistidae, Epermeniidae, Pyralidae, Pterophoridae, Noctuidae and Agaristidae, as well as nearly all butterflies, avoid *Eucalyptus* entirely or almost so.

This great dependence of Australian Lepidoptera and other insects on *Eucalyptus* is remarkable when it is realized that eucalypt foliage contains substantial amounts of essential oils (Penfold & Willis, 1961) and phenols, including tannins (Hillis, 1966; Fox & Macauley, 1977). Several workers in the Northern Hemisphere have shown that insects tend to avoid foliage with a substantial phenol content, but many Australian insects appear to have evolved a high degree of tolerance to these substances. For example, Fox & Macauley (1977) showed that *Paropsis* (Coleoptera) larvae ingested and grew normally on a diet of young eucalypt leaves containing more than 25% dry weight

of phenolic compounds, all of which passed through the gut unchanged and were recovered in the feces. They also showed that even young eucalypt leaves are extremely deficient in nitrogen, with levels ranging from 0.49% to 1.85%, compared with about 5% for young oak leaves. It seems clear therefore that many Australian insects, unlike their counterparts in the Northern Hemisphere, have become adapted to foodplants high in essential oils and phenols, and exceptionally low in nitrogen. Conversely, there are few if any of the introduced exotic insects in Australia that attack eucalypts or other typically Australian plants.

In addition to those species that feed on the living eucalypt tree, there are a great number that have adapted to feeding on fallen eucalypt leaves. Apart from such families as Tineidae and Blastobasidae, in which the larvae are frequently scavengers or detritus feeders, the larvae that depend on dead *Eucalyptus* leaves belong mainly to the Tortricidae and the Oecophoridae, but a few are found in the Gelechiidae, Xyloryctidae, Stathmopodidae, and Epipaschiinae (Pyralidae), and even in the Sterrhinae (Geometridae) and Hypeninae (Noctuidae). Some members of the Lecithoceridae are known to feed on dead eucalypt leaves and it is probable that the entire family is dependent on leaf litter. In recent studies on the composition of the leaf litter fauna in Australia a mean of 439 lepidopterous larvae per m^2 was reported (Plowman, 1979) from the litter in a wet sclerophyll eucalypt forest near Brisbane, and 99.8 larvae per m^2 in a mixed *Nothofagus-Eucalyptus* forest in Tasmania (Howard, 1975).

Large sections of the Australian Tortricidae and Oecophoridae have apparently co-evolved (Ehrlich & Raven, 1965) with the typically Australian plant communities, especially with the eucalypts. For the purposes of this discussion the family Oecophoridae is used in the sense of Common (1970). This is by far the largest Australian family of moths and includes more than 2000 named species and a further 1500 known species that are not yet described; it has an estimated total of 5500 Australian species. The named species have been referred to more than 290 nominal genera which, with synonymy, can be reduced to a maximum of 240 genera; with further revision there may prove to be less than 200 named genera. Most of these are endemic and many additional endemic genera await description. Only a few, mainly rainforest genera, are shared with New Guinea and south-east Asia and, in the present state of our knowledge, there appear to be few near relationships of the Australian fauna with that of New Zealand, South America or South Africa. The origin of the ancestral Australian Oecophoridae is unknown, but it seems clear that the extraordinary evolutionary radiation of this group occurred within Australia itself and

TABLE 1. Australian Oecophoridae and Tortricidae reared from *Eucalyptus*.

	Total reared	Number & percent of species on *Eucalyptus*					
		Living leaves		Dead leaves		All leaves	
TORTRICIDAE							
Total	199	13	(7%)	40	(20%)	53	(27%)
Tortricinae	141	9	(6%)	40	(28%)	49	(35%)
Olethreutinae	58	4	(7%)	—	—	4	(7%)
OECOPHORIDAE							
Total	322	79	(25%)	188	(61%)	267	(83%)
Depressariinae	16	3	(19%)	—	—	3	(19%)
Other subfamilies	306	76	(25%)	188	(61%)	264	(86%)

presumably paralleled the radiation in the characteristic Australian flora.

The Australian Tortricidae include 600 named species and a further 300 known species not yet described; a total of 1200 Australian species has been estimated for the family. Unlike the situation in most other regions, the Tortricinae outnumber the Olethreutinae. The number of Olethreutinae is probably comparable with that of other major areas of similar size, but well over 500 Australian Tortricinae are already known, of which only 360 are named, and the total is estimated at nearly 700. The difference in magnitude between the Australian representation of this subfamily and that in other regions may well be related to the adaptation of many Australian genera to the xerophytic sclerophyll plant communities, especially to *Eucalyptus*.

Of the 322 species of Australian Oecophoridae that have been reared, 79 (25%) are restricted to green *Eucalyptus* leaves, and 188 (61%) are dependent on dead eucalypt leaves (Table 1). Few, if any, of the dead leaf feeders belong to the Depressariinae, a group represented in Australia by only 21 named genera, nine of which appear to be restricted to rain forest. If the 322 oecophorid life histories constitute a representative sample of the family in Australia, we could expect to find a total of 4000 species dependent on *Eucalyptus*, and three-quarters of these dependent on dead eucalypt leaves.

Of the 200 species of Australian Tortricidae that have been reared, only 4 (7%) of the 58 Olethreutinae are restricted to living *Eucalyptus* foliage and 9 (6%) of the 141 Tortricinae. Whereas none of the reared Olethreutinae are known to feed on dead eucalypt leaves, 40 (28%) of the reared Tortricinae do so. In this respect the Australian Tortricinae are unique.

This remarkable development of dead-leaf feeding in the Australian Oecophoridae and Tortricidae may well be an adaptation to the physiological processes responsible for leaf-shedding in *Eucalyptus*. The length of time eucalypt leaves remain on the tree is surprisingly short for evergreen species and has been estimated to average no more than 18 months. However, the life of leaves is extremely variable depending on the species and the position of the leaves on the tree, and leaf-fall can be initiated by flowering or fruiting, by periodical bursts of growth in the tree, by insect attack, and by fire. After insect attack leaves are renewed from accessory buds and the older insect-damaged leaves are shed. At all seasons of the year eucalypts shed leaves, especially the mature leaves (Jacobs, 1955; Penfold & Willis, 1961). Here then, in the evolving eucalypt-dominated sclerophyll forests and woodlands, an abundant supply of leaf litter food, probably with a high phenol and a very low nitrogen content, awaited any organisms which had the genetic potential to occupy such a niche, a challenge that was squarely met by many Oecophoridae and Tortricinae.

In the Oecophoridae most of the species that feed on living *Eucalyptus* leaves utilize the mature foliage. It follows, therefore, that should the mature leaves harboring larvae be shed before the larvae have reached maturity, survival may well depend on the ability of each species to utilize wilting, partially dry or even completely dry foliage on the ground. Although the capacity to feed on fallen foliage has probably evolved many times in the Lepidoptera, it seems probable that in many of the Oecorphoridae, this was the mechanism which resulted in such a behavior pattern. In the genus *Ocystola*, for example, the larvae of some species feed on green *Eucalyptus* leaves, joining adjacent mature leaves in a characteristic fashion to produce a roomy cell in which the larva forms a flattened elliptical case of silk and fecal pellets. Feeding takes place within the cell on the surface tissue of the two leaves and pupation occurs in the enclosed case. In other closely related species of *Ocystola*, similarly joined recently dead leaves, with the larval case between, are commonly found on the ground beneath the eucalypts from which the leaves have been shed. Such larvae can continue to feed on the drying leaf tissue and emerge successfully as adults. The larvae of some other species of *Ocystola* feed throughout life on dead leaf litter. Other genera, or groups of closely related genera, provide similar examples.

One might suppose that leaf litter would provide a very uniform habitat, with little opportunity for the development of special adaptations and the application of selective pressures. However, in a semi-arid environment this is far from the truth, and the Australian Oecophoridae have developed many novel devices for survival. Desiccation

and extremes of temperature must seem almost insuperable barriers in the relatively harsh Australian environment, but the Oecophoridae have overcome these problems by constructing a wide range of larval cases or larval shelters, or other means to avoid or resist such hazards. In the genus *Garrha*, for example, the larvae live in portable lenticular cases usually found under leaf litter and feed at night. In situations in which the leaf litter is sparse and the diurnal temperatures are high, the larvae of some species attach the case with a few strands of silk vertically to a grass stem so that it is a few millimeters clear of the hot ground and the narrow edge of the case is oriented towards the sun, thus reducing the effects of radiant and conducted heat. The larvae of some species of oecophorids are also able to resist or avoid the effects of fire to some extent, their populations being restricted during hot and dry weather to slightly moist places beside the butts of trees, beside or under logs or stones, or in hollows in the ground or in dead stumps, or even under loose bark on tree trunks. And as long as the areas burnt are not too extensive, or as long as unburnt islands remain, some species can apparently respond to the abundant leaf-fall following the fire and rapidly re-establish in the burnt areas.

For long the life history of the litter-feeding Tortricinae was unknown, despite the fact that the adults of some are often very common. I first suspected that they may feed on green *Eucalyptus* leaves, perhaps high in the tree canopy where they may have been overlooked. After obtaining fertile egg masses from captured females, I offered the newly hatched larvae sandwiches of young freshly cut green eucalypt leaves. The young larvae quickly settled down in silken shelters between the leaves and fed readily. As the leaves deteriorated I carefully transferred the young larvae to fresh young leaves and in this way reared them successfully. However, I found that young larvae of the same species still continued to feed freely and reached maturity even if the original green leaves were not replaced, as long as they did not dry out completely. It seemed probable therefore that the larvae might be adapted to feeding on dead eucalypt leaves throughout life, and persistent search in the leaf litter subsequently yielded larvae of many species. As in the Oecophoridae, the larvae were not found to be generally distributed in the litter, but were restricted to microhabitats characteristic of each species. Hence, tortricine larvae occur amongst leaves which have accumulated in the hollowed-out tops of dead stumps, on logs, close to the butts of trees and stumps, amongst rocks, or behind loose bark on tree trunks. Some can be found most easily between joined dead leaves still adhering to recently fallen twigs and branches. At one stage I thought that such larvae may have been shed with the green leaves from the tree, but

this does not appear to be so. Over the litter, I randomly distributed a series of freshly cut twigs of *Eucalyptus*, each bearing about a dozen leaves; I then examined these 24 hours later and found several nearly mature *Meritastis* larvae between joined leaves on these freshly cut twigs. The larvae of this and other species are evidently quite mobile in the litter and are attracted to the freshly fallen leaves as food.

Major imbalances in the Australian fauna of Lepidoptera occur in those families which have the highest percentage of endemism and which are associated with diverse and relatively xerophytic plant communities. It seems very probable that these insect groups evolved along with the typically Australian plant communities with which they occur, and that similar selective factors were responsible for an extraordinary species radiation in both the xerophytic plant hosts and the insects dependent upon them.

Literature Cited

Common, I. F. B. 1970. Lepidoptera (Moths and butterflies). Pp. 765–866 *in* The Insects of Australia. Melbourne, Melbourne University Press. 1029 pp.

——— 1975. Evolution and classification of the Lepidoptera. Annu. Rev. Ent. 20: 183–203.

Ehrlich, P. R. & P. H. Raven. 1965. Butterflies and plants: a study in coevolution. Evolution 18: 586–608.

Fox, L. R. & B. J. Macauley. 1977. Insect grazing on *Eucalyptus* in response to variation in leaf tannins and nitrogen. Oecologia (Berl.) 29: 145–162.

Galloway, R. W. & E. M. Kemp. 1981. Late Cainozoic environments in Australia. *In* Biological Ecology of Australia (ed. A. Keast), in press.

Hillis, W. E. 1966. Polyphenols in the leaves of *Eucalyptus* L'Herit: a chemotaxonomic survey. I. Introduction and a study of the series Globulares. Phytochemistry 5: 1075–1090.

Howard, T. M. 1975. Litter fauna in *Nothofagus cunninghamii* forests. Proc. R. Soc. Vict. 87: 207–213.

Jacobs, M. R. 1955. Growth Habits of the Eucalypts. Canberra, Commonwealth Government Printer. 262 pp.

MacKay, M. R. 1970. Lepidoptera in Cretaceous amber. Science 167: 379–380.

Penfold, A. R. & J. L. Willis. 1961. The Eucalypts. New York, Wiley Interscience Publishers. 550 pp.

Plowman, K. P. 1979. Litter and soil fauna of two Australian subtropical forests. Aust. J. Ecol. 4: 87–104.

Pryor, L. D. 1959. Species distribution and association in *Eucalyptus*. Pp. 461–471 *in* A. Keast et al., eds. Biogeography and Ecology in Australia. Den Haag, Junk. 640 pp.

THE LIFE CYCLE OF *CHARAXES MARIEPS* (NYMPHALIDAE)

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ABSTRACT. The life cycle, oviposition preferences and larval foodplant preferences of *Charaxes marieps* Van Someren (Nymphalidae) are reported and discussed for the first time. Females were induced to oviposit on five species of plants belonging to the family Ochnaceae viz., *Ochna arborea*, *O. arborea* var. *oconnori*, *O. holstii*, *O. serrulata* and *O. natalitia*. The life cycle was studied using only *O. serrulata*, since larvae on the other four species of *Ochna* were discarded after completion of the second instar. The egg, larva and pupa of *C. marieps* as well as larval foodplant preferences were found to be very similar to those described for *C. karkloof karkloof* indicating that they are closely related species, even though they are geographically separated by some 300 km.

The life cycles of many South African *Charaxes* are well known (Dickson & Kroon, 1978). The general aspects of the life histories of some of these have been discussed by Henning (1977). However, the life history of *Charaxes marieps* (Van Someren & Jackson, 1957) has not been thoroughly investigated. This species is endemic to the Republic of South Africa, where it is confined to the montane forests of the eastern Transvaal. It belongs to a group of closely related species referred to as the "black" *Charaxes* complex, in which the males of the various species have the uppersides of the wings almost uniformly velvety-black (Dickson & Kroon, 1978). Other members of this complex occurring in South Africa include *Charaxes phaeus* (Hewitson), *C. vansoni* (Van Someren), *C. ethalion ethalion* (Boisduval), *C. pondoensis* (Van Someren), *C. karkloof karkloof* (Van Someren & Jackson) and *C. karkloof capensis* (Van Someren). The first two species are inhabitants of the arid Bushveld, to which their foodplants are restricted (Acocks, 1975). *C. ethalion ethalion* occurs in the coastal forests of Natal and Zululand, as well as in the montane forests of the Zoutpansberg in the northern Transvaal. The life cycle of this species has been recorded by Clark (unpublished data). *C. pondoensis* is found only in the coastal forests of the Transkei and its life cycle is unknown. *C. karkloof karkloof* inhabits the montane forests of central Natal, extending southward to the coastal forests of the Transkei. The only recorded foodplant for this species is *Ochna arborea* (Burch ex DC). The early stages of this species have been described by Van Someren (1966). *C. karkloof capensis* occurs in the coastal forests of the southern Cape Province, but nothing is known of its life cycle.

Although the natural habitat of *C. marieps* is vegetationally and climatically similar to the montane forests of Natal, where *C. k. karkloof* occurs, and to the Zoutpansberg forests where *C. e. ethalion* flies,

neither of these species have been recorded flying together with *C. marieps*. Morphologically, the imagines of *C. e. ethalion* are quite distinct from *C. marieps,* but *C. k. karkloof* closely resembles the latter. Because of these similarities between *C. k. karkloof* and *C. marieps,* as well as their habitat preferences and the fact that *C. k. karkloof* is known to utilize *Ochna arborea* as a foodplant, various *Ochna* species were used in our breeding trials with *C. marieps.*

The larval foodplant preferences and life cycle of *C. marieps* have not been recorded prior to this study. The purpose of this paper is to present, for the first time, data on the life cycle, oviposition preferences and foodplant acceptability of *C. marieps.*

Materials and Methods

For the breeding experiments with *C. marieps* six females were collected from the type locality at Marieps Kop, eastern Transvaal, in March 1978. Because it was suspected that *C. marieps* may utilize *Ochna* species as foodplants, the type locality was searched for the presence of *Ochna* species, as well as for eggs and larvae.

Captured females were housed separately in transparent plastic boxes and were fed once daily. Each female was offered a predetermined species of foodplant, *Ochna arborea, O. arborea* var. *oconnori, O. holstii* or *O. serrulata.* Two females were offered *O. natalitia.* Fresh leaves were provided daily and these were examined for eggs upon removal from the boxes. As eggs were found they were transferred to separate plastic containers.

Newly-hatched larvae were sleeved on the corresponding plant on which the eggs were laid and were kept at ambient temperature. Because only *O. serrulata* was available in large enough quantities to ensure completion of all the larval stages, larvae on the other four species of *Ochna* were discarded after completion of the second instar.

Larvae on *O. serrulata* were examined twice daily and their growth and coloration as well as the duration of larval, prepupal and pupal stages were noted. Daily temperature ranges during the rearing period were recorded. Some eggs and first instar larvae were collected and prepared for scanning electron microscopy by critical point drying and sputter coating with gold.

Two larvae from each instar were collected from *O. serrulata* and were killed in a 1:1 alcohol-xylene mixture. Next they were transferred to Pempel's fluid. Larvae were examined with a stereomicroscope and were drawn with the aid of a camera lucida.

RESULTS

Life Cycle

Egg. Subspherical, top and base flattened, 1.5 mm high, 2 mm diameter. About 30 longitudinal ridges made up of small tubercles, crowded at the top and disappearing towards the base (Fig. 1). Pale yellow when laid, developing a brown ring in upper third after 48 h. Larva hatches after 6–9 days and consumes entire egg shell.

First instar. 3–4 mm long; body creamy-yellow turning pale green after the first feeding. Headshield and anal appendages black with rusty-brown edges in some individuals. Headshield diameter 1–1.5 mm; dorsal horns 0.75–0.85 mm, curving inwards and backwards; lateral horns 0.4–0.5 mm, curving slightly upwards (Figs. 2, 3 & 8). Frons and clypeus pitted; horns bear numerous setated tubercles (Fig. 2). Body surface densely tuberculated (Fig. 3) and uniformly green. First instar lasts 8–23 days during which a length of 6–7 mm is attained.

Second instar. (Figs. 4 & 9). Body immaculate green; headshield and anal appendages dark brown. Dorsal horns 1.1–1.3 mm; lateral horns 0.7–0.8 mm, both dark brown with white tips. Frons and clypeus less densely pitted and horns less densely tuberculated than first instar. Body tubercles more widely spaced with white-tipped tubercles at base of anal appendages forming distinct pattern. length of 10–12 mm is attained in 20–35 days.

Third instar. (Figs. 5 & 10). Body light green; headshield 2.2–2.8 mm in diameter, brown with variable amount of green invading frons. Dorsal and lateral horns brown to ochre, white-tipped. Body tubercles green but a number of white-tipped tubercles scattered over body in definite pattern. Paired, white-tipped larger tubercles on either side of dorsal vessel. Towards end of instar a pair of purple dots appear dorsally on segment six. Third instar lasts 18–76 days; length attained, 14–16 mm.

Fourth instar. (Figs. 6 & 11). Headshield 3.5–4.2 mm in diameter, green with brown or ochre border. Dorsal horns (2.2–3 mm) and lateral horns (1.5–2 mm) green at base, brown distally and white-tipped. Body tubercles variable in size, larger ones white-tipped. Paired dorsal purple spots on segments six and eight, latter developing towards end of instar. Pleural fold distinct, consisting of white tubercles. Fourth instar lasts a minimum of 23 days; length attained, 22–25 mm.

Fifth instar. (Figs. 7 & 12). Headshield 5–6 mm in diameter, pale green, bordered by thin yellow or brown line. Dorsal horns 3–3.5 mm; lateral horns 2.5–3 mm, coloration as in fourth instar. Body pale green, numerous white-tipped tubercles, purple spots on segments six and eight distinct, latter often bordered by white patch. In some larvae only one or no spots on segment eight. Pleural fold light yellow. Minimum duration of fifth instar 56 days (winter); length attained, 32–42 mm.

Prepupa. C-shaped, pale translucent green, lasting 42–50 h.

Pupa. (Fig. 13). Pale green; margins of wing cases white or creamy-yellow; spiracles bordered by white. Pupal stage lasts a minimum of 15 days.

Imagines. (Figs. 14–17). Conform to description of Van Someren & Jackson (1957). In these trials females with russet wing margins occurred more often than those with wing margins the same as the ground color. Bred male imagines have wingspan of 60–64 mm; females 66–72 mm.

Oviposition Preferences

Careful searching of the type locality at the time the females were collected revealed that *O. arborea* var. *oconnori* and *O. natalitia* occur fairly abundantly and *O. holstii* and *O. serrulata* occur in smaller numbers. No eggs or larvae could be found on any of the plants searched. In our experiments the females of *C. marieps* did not show a preference for any specific *Ochna* species. Eggs were laid in more or less equal numbers on all the species of foodplant offered.
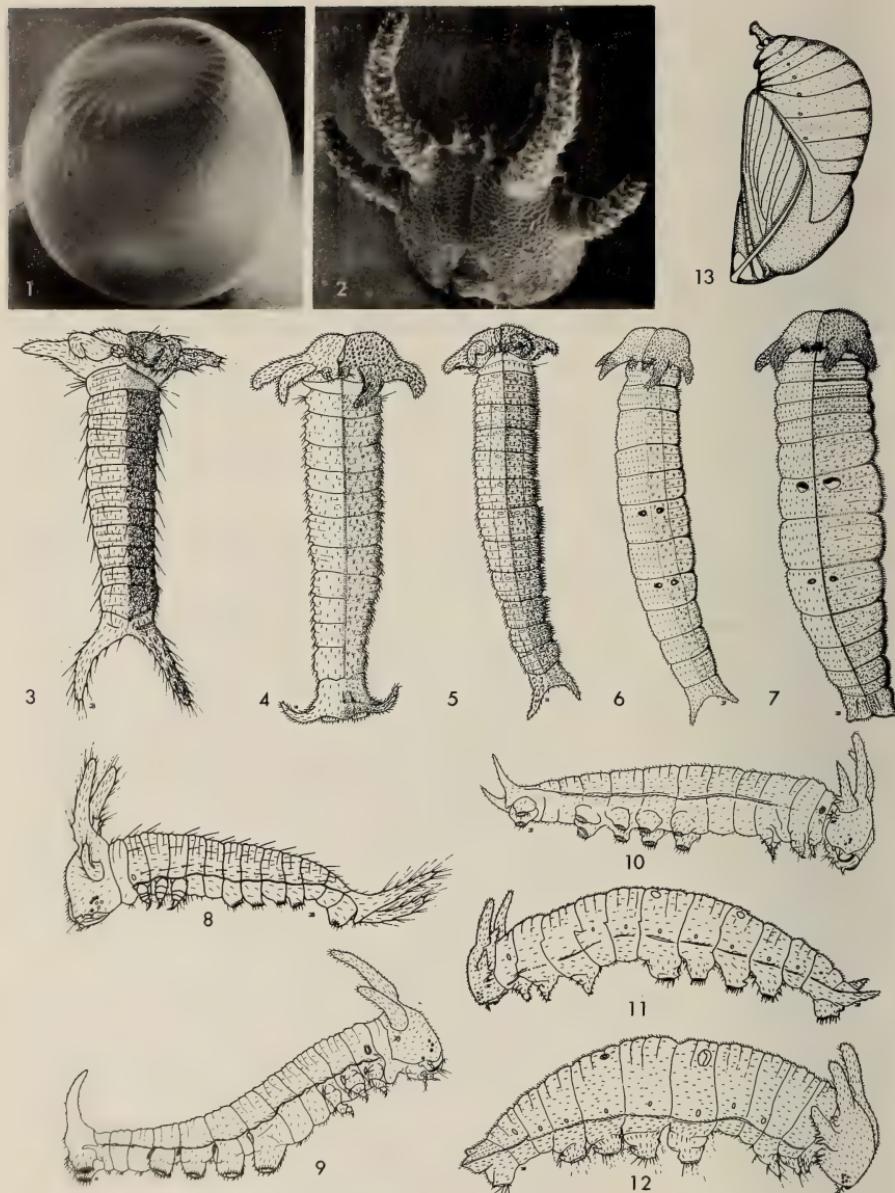
FIGS. 1–13. Egg and juvenile stages of *Charaxes marieps*. **1,** scanning electron micrograph of egg, ×60; **2,** scanning electron micrograph of first instar larval head-shield, ×60; **3,** first larval instar, dorsal view; **4,** second larval instar, dorsal view; **5,** third larval instar, dorsal view; **6,** fourth larval instar, dorsal view; **7,** final larval instar, dorsal view; **8,** first larval instar, lateral view; **9,** second larval instar, lateral view; **10,** third larval instar, lateral view; **11,** fourth larval instar, lateral view; **12,** final larval instar, lateral view; **13,** pupa, lateral view.

FIGS. 14–17. Imagines of *C. marieps*. **14,** ♂ upperside; **15,** ♀ upperside; **16,** ♂ underside; **17,** ♀ underside.

Foodplant Acceptability

All of the foodplants offered to the larvae were readily accepted. First and second larval instars were completed in about the same time irrespective of the particular foodplant used. Measurements of larvae on all *Ochna* species fell within the ranges given above.

DISCUSSION

Most of the members of the genus *Charaxes* utilize the foliage of trees belonging to a number of families as larval foodplants (Dickson & Kroon, 1978). In the case of South African members of the "black" *Charaxes* complex, where the foodplants are known, these mainly

belong to the large family Leguminosae (Henning, 1977). *Charaxes marieps* and *C. k. karkloof,* also belonging to the "black" *Charaxes* complex, are exceptions in that they utilize members of the family *Ochnaceae.*

Although the Ochna family is a large one (some 30 genera and more than 300 species are known worldwide) only one genus, *Ochna,* with about 9 species, occurs in South Africa (Palmer & Pitman, 1972). Of these, *O. arborea* var. *oconnori, O. holstii, O. natalitia* and *O. serrulata* occur in the known habitats of *C. marieps.* Our findings that captive females oviposited on these, as well as on *O. arborea* from Natal, and that larvae accepted all of these species as foodplants, suggest that the foliage of various *Ochna* species is probably similar in chemical composition. Unfortunately, because no eggs or larvae were found on any of the *Ochna* species at the type locality, it is not possible to say which are utilized in the wild. Since the distribution of the various *Ochna* species covers most of the eastern half of South Africa other factors presumably are responsible for the restriction of *C. marieps* to the high montane forests of a relatively small area of the eastern Transvaal escarpment.

The egg, larva and pupa of *C. marieps* are very similar to those of *C. k. karkloof,* judging from the short description by Van Someren (1966) and from personal observations. There is little doubt that these two species are closely related, despite their geographical separation.

From the examination of our own and other collections it would appear that females of *C. marieps* with russet wing edges are more often captured in spring (Sept. to Nov.). This may explain why all the females in our bred series have this coloration (hatched Sept. to Nov.). We postulate that low humidity, low temperature (or both) may be responsible for this slight seasonal dimorphism in females.

Charaxes spp. caught in spring in Southern Africa are smaller than those taken in late summer (Feb. to April). We assume that this is also true for *C. marieps* and that it may explain the discrepancy in size between our bred specimens (males, 60–64 mm; females, 66–72 mm) and wild caught specimens (males, 65 mm; females, 75 mm). The smaller spring specimens result from larvae that have fed during winter, whereas late summer hatchings represent larvae which have had the benefit of the more favorable environmental conditions during summer.

LITERATURE CITED

ACOCKS, J. P. H. 1975. Veld types of South Africa. (Memoirs of the Botanical Survey of South Africa, no. 40), Ed. D. J. B. Killick. Bot. Res. Inst., Dept. of Agricultural Technical Services, R.S.A.

DICKSON, C. G. C. & D. M. KROON. 1978. Pennington's Butterflies of Southern Africa. London, A. D. Donker Ltd.
HENNING, G. A. 1977. Observations on the early stages of Ethiopian *Charaxes* with notes on life histories (Lepidoptera: Nymphalidae). Ann. Transvaal Mus. 30: 219–230.
PALMER, E. & N. PITMAN. 1972. Trees of Southern Africa, Vol. 3. Cape Town, R.S.A., A. A. Balkema.
VAN SOMEREN, V. G. L. 1966–1967. Revisional notes on African *Charaxes* (Lepidoptera: Nymphalidae). Bull. Brit. Mus. Nat. Hist. (Ent.) 18: 47–101.
——— & T. H. E. JACKSON. 1957. The *Charaxes etheocles-ethalion* complex (Lepidoptera: Nymphalidae). Ann. Transvaal Mus. 23: 41–58.

NEW STATUS FOR *EUMORPHA INTERMEDIA* (SPHINGIDAE)

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ABSTRACT. *Eumorpha intermedia* (Clark) is elevated to the status of a full species. Evidence based on differences in size, color, maculation and genital characteristics shows that it is not a subspecies or form of *E. satellitia* (Linnaeus) or *E. pandorus* (Hubner) as previously considered. *E. intermedia* is described, illustrated and compared with ten related species and subspecies.

In The Moths of America North of Mexico, Fascicle 21, Sphingoidea, *Pholus satellitia intermedia* Clark, 1917 (Proc. New England Zoological Club, 6: 67. Type locality: Baton Rouge, Louisiana) was treated as synonymous with *Eumorpha pandorus* (Hubner). Hodges (1971: 123) stated "Clark described *intermedia* which was later treated as a subspecies of *satellitia*." In synonymizing the subspecies *E. satellitia ampelophaga* (Walker) and *E. satellitia intermedia* (Clark) with *E. pandorus* (Hubner), however, Hodges (1971: 124) did not fully cite Clark's original description, thus implying that *intermedia* was described as a species. Clark described *intermedia* as a subspecies of *E. satellitia* (L.).

Eumorpha intermedia Clark, new status

Fig. 1

Size differences. Based on measurements of 65 specimens of *intermedia* from Louisiana and Mississippi and 309 *pandorus* from most of its range in North America, *intermedia* is ten percent smaller in size than *pandorus*. The average wing length for males of *intermedia* is 40 mm (range: 38–41 mm). The average wing length of females is 44 mm (range: 43–47 mm). Clark listed the wing length of the male as 38 mm and the female as 44 mm. *Intermedia* is the smallest species of *Eumorpha* in America north of Mexico.

Types. The designated types, one male and one female, were collected at Baton Rouge, East Baton Rouge Parish, Louisiana. One male from Greenville, Washington Co., Mississippi and one female from Brownsville, Cameron Co., Texas were listed as cotypes. The cotypes are in the U.S. National Museum.

Wing pattern. Of the species mentioned herein, the maculation of *intermedia* is nearest to that of *pandorus, satellitia satellitia* and *satellitia analis* (Rothschild & Jordan), but with distinct differences. Clark (1917) differentiated between *intermedia* and related species, namely: *E. licaon* (Cramer) (=*E. satellitia*, according to Hodges, 1971), *E. elisa* (Smyth) and *E. pandorus* by color and maculation. I have examined and compared the following similar species on the basis of color and maculation. All are distinguishable by these attributes. The species are: *E. elisa*—8 specimens, *E. satellitia satellitia*—342 specimens, *E. pandorus*—309 specimens, *E. satellitia analis*—28 specimens, *E. satellitia excessus* (Gehlen)—3 specimens, *E. satellitia posticatus* (Grote)—

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FIG. 1. *Eumorpha intermdia* ♀, 20 June 1979, Edgard, Louisiana.

1 specimen, *E. satellitia rosea* (Closs)—5 specimens, *E. eacus* (Cramer)—1 specimen, *E. anchemola* (Cramer)—50 specimens, *E. triangulum* (Rothschild & Jordan)—92 specimens.

Intermedia differs in color and maculation from the taxa with which it was compared as follows (Fig. 1): **Above,** fresh specimens are medium to dark olive-brown with darker shading and tinted with a deep olivaceous and pinkish hue. In worn or old specimens, the deep olive color fades. Dried specimens have a tendency to become lighter in color with age.

The **upper surface** of the **forewing** bears a dark, subapical, triangular patch on the costal margin, truncate inwardly at vein R_5. A similar triangular patch is located on the inner margin near the anal angle, the apex approaching vein Cu_1. The outer side of this patch is indented in cell Cu_2 as in other species mentioned herein except *pandorus*. (Among the 309 *pandorus* studied, 3 ♂ specimens exhibited this indentation characteristic). Along the center of the inner margin is a very dark rhombiform median patch, extending to the base in a slightly lighter olive-brown shade. The distal edge of this patch curves strongly basad near the inner margin, where it is defined by whitish scales [as in *E. anchemola*, for example], unlike the other species being compared, where the edge of the patch is straight and meets the inner margin obliquely, and where the patch is not bounded along the inner margin by whitish scales. The end of the cell bears a conspicuous double stigma. A slightly darkened area extends distad of a line between middle of the costal margin and a point two-thirds the distance from the apex to the anal angle. The point at which the inner edge of this area intersects the costal margin is more basad than in *pandorus*. From the apex of the rhombiform patch, two roughly parallel median lines extend anteriorly and curve inwardly through this

FIG. 2. **a,** *Eumorpha pandorus,* ♂ genitalia; **b,** *Eumorpha intermedia,* ♂ genitalia.

FIG. 3.   Range of *Eumorpha intermedia* based on verified specimens.

dark area to the costal margin. The subterminal lines are distinctly scalloped near the apex of the forewing. In *pandorus*, these lines are slightly wavy approaching the apex. Veins Cu_1 and Cu_2 of *intermedia* are conspicuously pink, especially Cu_1, as in *pandorus*.

On the **upper surface** of the **hindwing,** there is a large median patch near the inner margin. It is bordered basally and anteriorly with light yellow-brown. A submarginal series of usually three or four very dark spots extends outward from near the anal angle and diffuses distally. The spots are much broader than in *pandorus,* more like those of *satellitia satellitia* and *satellitia analis*. A distinct pink line inwardly borders the submarginal spots and becomes obscure distally. The light outer margin band of *pandorus* is absent in *intermedia*. The anal angle is light pink, usually to an equal or greater degree than in *pandorus* or *satellitia satellitia,* but never the deep red color of *satellitia analis* or *satellitia posticatus*.

Below, *intermedia* is reddish-brown. In fresh specimens, rosy coloration is dominant on the wings and ventral portion of the abdomen. In worn and faded specimens, this rosy cast can be faint to non-existent. The **underside** of the **forewing** has a gray band along the distal margin. Somewhat parallel to the distal margin, the median and postmedian lines curve inward to meet the costal margin. The **underside** of the **hindwing** has a similar gray band along the distal margin and parallel lines turning basally as on the forewing.

Genitalia.   In comparing the genitalia of a series of Louisiana and Mississippi specimens of *intermedia* and *pandorus,* there are consistent differences (Figs. 2a, 2b). In the male genitalia of *intermedia*, the uncus is curved more than in *pandorus* and is 3 mm in length. The aedeagus is 5.5 mm, one-third shorter in length than that of *pandorus*. The saccus is drastically reduced, 1.5 mm in length, four-tenths the size of that of *pandorus*.

In the female genitalia, the corpus bursae of *intermedia* is smooth on the outer surface, rather than ribbed as in *pandorus*. It is twenty percent smaller in size than that of *pandorus*. The apophyses posteriores are shorter in *intermedia* by thirty percent.

Range. In A. Seitz, M. Draudt (1931) indicates the range of *intermedia* to be "Gulf States, west to New Mexico." The following records of verified specimens exhibit the currently known range and flight periods of *intermedia* (Fig. 3). North Carolina: 1 specimen, Carteret Co., August. South Carolina: 3 specimens, Charleston Co., August. Georgia: 1 specimen, Screven Co., August. Florida: 2 specimens, Gadsden and Alachua Counties, July. Mississippi: 19 specimens, Bolivar, Warren and Hancock Counties, June through September. Louisiana: 60 specimens, Ascension, East Baton Rouge, East Feliciana, Ibberville, Orleans, St. Charles, St. John the Baptist and West Feliciana Parishes, April through October. Texas: 11 specimens, Brownsville, Cameron Co., April, May, June, July and October.

ACKNOWLEDGMENTS

LITERATURE CITED

CLARK, B. P. 1917. New Sphingidae. Proc. New England Zool. Cl. 6: 67–68.

DRAUDT, M. 1931. Familie Sphingidae. *In* A. Seitz: Die Gross-Schmetterlinge der Erde 6: 882.

HODGES, R. W. 1971. The Moths of America North of Mexico, Fasc. 21, Sphingoidea, 123–124.

Note added in proof: The range of *Eumorpha intermedia*, based on verified specimens, has been extended westward to include Webster Parish in northwestern Louisiana.

EGG-LOAD ASSESSMENT AND CARRYOVER DIAPAUSE IN *ANTHOCHARIS* (PIERIDAE)

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ABSTRACT. At Gates Canyon, California, *Anthocharis sara* overdisperses its eggs, showing apparent egg-load assessment. *Pieris napi microstriata* at the same site shows a more typical contagious egg distribution. Pupae of *A. sara* frequently carry over into a second or third year of diapause in captivity. Similar phenomena apparently occur in *A. midea* of the eastern U.S. Evolutionary interpretations of such phenomena tend to overestimate "fine tuning" to local environments, but interspecific comparisons may reveal much broader patterns.

The life-history characteristics of insects are receiving increasing attention as theoretical models of such aspects as phenology, diapause and reproductive effort become common (Levins, 1969; Cohen, 1970; Giesel, 1976). The leaf- and inflorescence-feeding guilds of pierid butterflies offer excellent opportunities for studies of life-history phenomena as they affect both population and community ecology. This paper reports upon two ecologically important aspects of the life-history of the Sara Orange Tip, *Anthocharis sara* Lucas, in riparian woodland at Gates Canyon, Vaca Mts. (Inner Coast Range), Solano Co., north-central California (50–600 m).

Egg-load Assessment

"Egg-load assessment" means a female's choice to oviposit or not on a given plant is influenced by whether or not eggs (con- or heterospecific) are already present. The feedback may be negative (leading to overdispersion of eggs) or positive (leading to aggregation); usually the former is meant.

Rothschild and Schoonhoven (1977) obtained laboratory evidence that *Pieris brassicae* (L.), which lays its eggs in large clusters, and perhaps *P. rapae* (L.), which lays them singly, are capable of recognizing conspecific eggs on host plants and adjusting their oviposition behavior, presumably to avoid host overload. This is an appealing idea, although like most density-related factors influencing population density it is bound to be controversial. There is no evidence of such prudence in earlier studies of temperate butterflies (Dethier, 1959). The distribution of *P. rapae* eggs has been studied on field cabbages by Harcourt (1961), Kobayashi (1965 and earlier papers), and Jones (1977); all found contagious (negative binomial) distributions of eggs, arguing strongly against egg-load assessment by that species. Jones (1977) successfully modeled its oviposition behavior while specifically excluding egg-load assessment.

TABLE 1. Distribution of pierid eggs on *Barbarea verna* at Gates Canyon, California, 1973 through 1978 (pooled data), excluding 1977.

Number of eggs/plant	Size class of plant			
	Large	Medium	Small	Totals
Anthocharis sara				
0	154	202	46	402
1	90	138	35	263
2	24	20	2	46
3	1	2	0	3
Totals:	269	362	83	714
x̄ (eggs/plant):	0.52	0.57	0.47	0.51
s^2:	0.45	0.40	0.30	0.41
Mean eggs/plant with any eggs at all:				1.17
Pieris napi microstriata				
0	198	258	57	513
1	23	35	11	69
2	15	23	5	43
3	12	11	4	27
4	10	17	2	29
5	6	13	3	22
6	1	3	1	5
7	3	1	0	4
8	1	1	0	2
Totals:	269	362	83	714
x̄ (eggs/plant):				0.75
Mean eggs/plant with any eggs at all:				2.67

Whether or not assessment is a reality in either of these *Pieris*, egg censuses on pierids in California localities which have been under study for several years offer an opportunity to look for statistical evidence of it in others. The best data are for Gates Canyon.

Anthocharis sara deposits its eggs singly near the tops of Crucifers in riparian habitat—usually on stems, pedicels, or the bases of petioles, less often on buds, flowers, or leaves. They are initially creamy white, but rapidly turn orange, becoming conspicuous and easily censused. At Gates the principal host is *Barbarea verna* (Mill.) Asch. Table 1 presents egg counts of *A. sara* and of *Pieris napi microstriata* Comstock on 714 individual plants censused between 1973 and 1978, excluding 1977 (see below). Newly-laid *sara* eggs are distinguishable from *napi* by shape, while older ones are easily recognized by color. These two butterflies are sympatric and synchronic at Gates and feed on the same hosts, but *napi* is a leaf feeder while *sara* consumes

inflorescences and especially green fruit. Numbers of *napi* are more variable from year to year than those of *sara*, and this is reflected in the pooled 1973–78 data in which some 200 *napi* eggs are from its peak year of 1976 alone. The *napi* data are included as a contrast to *A. sara* in the context of their joint use of *Barbarea*.

The *Barbarea* plants have been grouped into three arbitrary size classes which incorporated information on both height and shape of plant (number of stems). Egg dispersion was analyzed statistically for each species on each size class and for the pooled plants. The eggs of *P. napi* are contagiously distributed in all cases, and the statistical properties of their distributions need not concern us here. For *A. sara* the means of the distributions all exceed their respective variances, implying some degree of overdispersion and hence of egg-load assessment. When the distributions are compared to Poisson series by a χ^2 test, medium and small plants both differ significantly ($P < .005$) while large ones do not ($.500 > P > .250$). This suggests that egg-load assessment is on a per-inflorescence, not a per-plant basis and breaks down when many stems are available. Unfortunately, this is not testable with these data as only plant totals were recorded. It is however, definitely occurring in some related species which oviposit in inflorescences (Shapiro, 1981). On the other hand, medium plants are preferred to large ones since about equal numbers of eggs are deposited on both although the biomass of the large plants is much greater. *A. sara* is a more efficient searcher than *P. napi*, since 44% of the plants received at least one *sara* egg *vs.* 28% with *napi* eggs; *napi*, however, lays more eggs per plant receiving any eggs.

To what extent are these patterns influenced by plant density and dispersion? The spatial distribution and conspicuousness of the host plant may have important, and sometimes subtle, impact on oviposition behavior (cf. Thompson & Price, 1977). The *Barbarea* plants at Gates Canyon are distributed in a nearly linear canyon-bottom environment, and an ovipositing *A. sara* is almost always in sight of other plants. Thus the likelihood of her finding the same plant after her seemingly obligatory interovipositional flight is quite low. Data collected in 1979 from isolated hosts surrounded by unfavorable grassland and chaparral environments (Shapiro, 1981) provide an additional clue. On such plants egg-load assessment seems to occur only by subsequent females after the eggs have darkened. Individual females may oviposit repeatedly on the same plant, with an intervening flight between each oviposition and the next. The overdispersion observed at Gates can then be viewed as a two-part phenomenon: a given female can overdisperse her eggs only if sufficient hosts are available nearby, but later females may be obliged behaviorally to

TABLE 2. Distribution of *Anthocharis sara* eggs on *Barbarea verna* at Gates Canyon, California in 1977.

Number of eggs/plant	Size class of plant			
	Large	Medium	Small	Totals
0	4	19	40	63
1	2	9	12	23
2	1	5	1	7
3	0	1	0	1
Totals:	7	34	53	94
			x̄ (eggs/plant):	0.43
			Mean eggs/plant with any eggs at all:	0.78

defer to her darkened eggs whatever the host dispersion. The growing literature of egg-load assessment is reviewed and compared to a variety of data on various pierids by Shapiro (1981). It should be explicitly noted that interovipositional flights occur in most or all pierids which do not lay eggs in batches, whether or not egg-load assessment is suspected. The degree to which both phenomena are developed, coupled or decoupled, presumably reflects the relative strength of such selective forces as intra- and interspecific competition, predation, and parasitism, and in particular their spatial and temporal predictability.

Interspecific Interaction

1977 was the second year of severe drought in California, and biomass of *Barbarea* was reduced by an estimated order of magnitude at Gates. The number of plants was reduced, and only seven "large" plants could be found. Faced with this highly atypical host distribution, *A. sara* found only 33% of the plants—but its egg distribution did not change significantly $(.500 > P > .250)$ (Table 2). *P. napi* was virtually absent in 1977 (only 1 egg was found). Did this affect *A. sara* in any detectable way? In 1973–78 (except 1977) there was some degree of positive association of the two species on individual plants (Table 3). This is presumably due to similar enough searching behavior to make the same individual plants especially attractive to females of both, rather than to a positive response *per se* to each other's eggs. This interpretation is bolstered by the observation that the same individual plants, or plants in the same locations, receive or do not receive eggs year after year. Due to egg-load assessment, *A. sara* is obliged to spread its eggs more widely, finding many more plants missed by *napi* than the converse. There is no indication that the presence or absence of *napi* affects *sara* at all.

Table 3. Measures of association between *Anthocharis sara* and *Pieris napi microstriata* at Gates Canyon, 1973–78 except 1977.

	Size class of plant		
	Large	Medium	Small
Expected # plants jointly occupied if independent	31.1	46.2	11.6
Observed # plants jointly occupied	39	63	10
χ^2	5.84	15.87	0.57
P	.025 > P > .010	P < .005	.500 > P > .250 (N.S.)
Cole's index of association (Cole, 1949)[a]	+0.285	+0.371	−0.050
Mean # eggs laid by *sara* on plants without *napi*	0.477	0.418	0.492
Mean # eggs laid by *sara* on plants with *napi*	0.690	0.731	0.500
Significantly different?[b]	yes	yes	no
Mean # eggs laid by *napi* on plants without *sara*	0.474	0.475	0.848
Mean # eggs laid by *napi* on plants with *sara*	1.052	1.125	0.622
Significantly different?[b]	yes	yes	no

[a] Values range from +1 (completely associated) to −1 (completely negatively associated); 0 is independent.
[b] Student's t-test.

Egg-load assessment is a form of contest competition akin to territoriality. The first female to oviposit on an inflorescence reserves it for her young, excluding any other individual which participates in assessment. The shortage of oviposition sites in 1977 could have led to at least three different responses by *A. sara,* or combinations of them: (1) longer-range dispersal of females beyond the study area; (2) increased searching efficiency with more use of normally unused plants; (3) increased willingness to oviposit multiply on normally used plants. There is no direct evidence that any of these occurred; the egg data argue strongly against (3) and give no support to (2), while there are no adult data bearing on (1). The total egg output in 1977 was somewhat lower than in some preceding and following years, but this could be due to decreased fecundity or life-span rather than to dispersal. The 1979 data on isolated plants supported alternative (3) above, at least for individual (but not subsequent, post-egg-darkening) females, but here the host density was very much lower than at Gates even under the severe stress of 1977. The ratio of females to plants apparently did not pass the threshold at which same-day multiple ovipositions would at least partly nullify egg-load assessment.

Table 4. Developmental times of *Anthocharis sara* pupae from Gates Canyon, rared *ex ovo* on continuous light at 25°C, stored at 3°C. All were in diapause.

Year	Number of hatching after time at 3°:		
	Following spring	Second	Third or more[a]
1973	3	5	3
1974	6	8	5
1975	0	4	2
1976	0	9	3
1977	3	5[b]	—
Totals:	12	31	13

[a] Includes pupae which died after 2 years of storage.
[b] Includes all pupae uneclosed as of spring, 1978.

Carryover Pupae

Most uni- or bivoltine pierids have a mandatory chilling requirement to break pupal diapause, and will not eclose without a period of refrigeration. If held at room temperature they may live several years before expiring. Most pupae will eclose if held near 0°C for 9–10 months, but in any brood some may require a second or even a third year of chilling. The incidence of such carryover pupae, and their relation to environmental conditions during rearing, are uninvestigated. They are of interest because they may provide a "hedge" against population extinction due to a single catastrophic season, analogous to the "seed bank" of the plant ecologist (Harper, 1977). Facultative bi- or trienniality in normally annual species is on its face highly adaptive in uncertain environments. Insofar as it lengthens the mean generation time it reduces r, the intrinsic rate of natural increase, and it should therefore carry a selective tradeoff. The higher the environmental uncertainty, the easier it becomes to account for pupal carryover in terms of individual, rather than group, selection. Its taxonomic distribution in Lepidoptera is reviewed by Powell (1974).

In multivoltine pierids generally, diapause can be inhibited by rearing on long days or continuous light at temperatures of 25°C. This does not work on the spring univoltines. Since 1973 several eggs of *A. sara* have been collected each year at Gates for lab rearing on this regime. All the resulting pupae have diapaused, despite the facultative bivoltinism of the population, and 76% have carried over beyond the first year (Table 4). The tendency to produce carryover pupae is thus great in this population.

Between 1973 and 1978 rainfall at Vacaville, at the mouth of Gates Canyon, varied between 95.78 and 23.32 cm/water year (July 1–June 30). As noted above, *Barbarea* biomass fluctuated by an order of mag-

nitude, and in one year *P. napi* was virtually absent. Yet numbers of adult *sara* were surprisingly constant, and so were egg counts. Do carryover pupae provide a buffer against environmental uncertainty for this species?

A counterpoint: *Anthocharis midea*

The eastern Falcate Orange Tip, *A. midea* (Hbn.), belongs to a different subgenus than *A. sara* and occurs in a region of much less climatic uncertainty. Like *A. sara*, however, it is a spring-univoltine Crucifer feeder (perhaps locally facultatively bivoltine southward, but this is disputed), even including *Barbarea verna* in its diet (dos Passos & Klots, 1969; Shapiro, unpubl.).

Clark (1932, p. 165–166) reviews H. F. Schönborn's correspondence with W. H. Edwards regarding this species. He "never found a larva in open fields, although the plant grows there in abundance in large patches. I always found them on isolated plants growing in places sparingly covered by ... trees." This is familiar to Californians who recognize the limitation of *A. sara* to riparian woodland and its failure, after 150 years, to colonize the immense stands of weedy mustards on the broad valley floors. Schönborn moreover "never found more than one egg on a plant," nor have I in eastern Pennsylvania and New Jersey (N ≃ 100). These egg distributions carry no statistical force, but their implications are obvious.

Dos Passos & Klots (1969) provide some data on carryover pupae. Of thirteen 1953 pupae, 6 emerged in 1954 and 7 in 1955. They quote C. E. Rummel as having reared a 3-year individual. Photoperiods and temperatures are not specified. In 1966 I reared 4 larvae from Brown's Mills, Burlington Co., N.J. under uncontrolled photoperiod and temperature, and all gave carryover pupae.

These fragmentary data are included to emphasize the danger inherent to inferring causality from apparent adaptation. Stearns (1977) reviewed the epistemological pitfalls of life-history theory and concluded that many of its "validations" are spurious. Pitelka & Van Valen (1974) said the same thing, adding that "many theories are true when their assumptions are not, but this can never be taken for granted."

Both egg-load assessment and pupal carryover, considered uniquely as attributes of the Gates Canyon population of *A. sara*, appear as good candidates for "finely-tuned" adaptations to host dispersion and climatic uncertainty in that particular locality, and the temptation to interpret them thus in the terms of current theory is strong. When *A. midea* is also considered, the "fine-tuning" hypothesis becomes less appealing: the ecologies of the two species are quite different, while

their obvious commonality is genetic. Both egg-load assessment and pupal carryover may be derived by both species from a common ancestor; both *may* be preadaptive in current ecological contexts, but perhaps not. (One need not belabor the difficulties in establishing that X is *the* function of some attribute of an organism.) The subgenus *Falcapica*, which includes *midea* and *lanceolata* Lucas of the Pacific slope and is not really distinguishable from *Paramidea* of East Asia (*scolymus* Butler and *bieti* Oberth.), shows a classic Arcto-Tertiary relict distribution. The subgenus *Anthocharis*, to which *sara* belongs, is disjunctly distributed in western North America and the Palaearctic region (mostly western) and is also probably Arcto-Tertiary. We are beginning to talk about common ancestors of no small antiquity. Moreover, the related genus *Euchloe*, which also shows an Arcto-Tertiary pattern of dispersion, assesses egg load and has carryover pupae as well (Shapiro, in prep.), pushing the common origin of these phenomena back even further in time.

ACKNOWLEDGMENTS

LITERATURE CITED

CLARK, A. H. 1932. The butterflies of the District of Columbia and vicinity. Bull. U.S. Natl. Mus. 157: 1–337.

COHEN, D. 1970. A theoretical model for the optimal timing of diapause. Am. Nat. 104: 389–400.

COLE, L. C. 1949. The measurement of interspecific association. Ecology 30: 411–424.

DETHIER, V. G. 1959. Egg-laying habits of Lepidoptera in relation to available food. Canad. Entomol. 91: 554–561.

DOS PASSOS, C. F. & A. B. KLOTS. 1969. The systematics of *Anthocharis midea* Hübner (Lepidoptera: Pieridae). Entomol. Amer. 45: 1–34.

GIESEL, J. T. 1976. Reproductive strategies as adaptations to life in temporally heterogeneous environments. Annu. Rev. Ecol. Syst. 7: 57–79.

HARCOURT, D. G. 1961. Spatial pattern of the imported cabbageworm, *Pieris rapae* L., on cultivated Crucifers. Canad. Entomol. 93: 945–952.

HARPER, J. L. 1977. Population Biology of Plants. Academic Press, London. 892 pp.

JONES, R. E. 1977. Movement patterns and egg distribution in cabbage butterflies. J. Anim. Ecol. 46: 195–212.

KOBAYASHI, S. 1965. Influence of parental density on the distribution pattern of eggs in the common cabbage butterfly *Pieris rapae crucivora*. Res. Popul. Ecol. (Kyoto) 7: 109–117.

LEVINS, R. 1969. Dormancy as an adaptive strategy. Symp. Soc. Exptl. Biol. 23: 1–10.

PITELKA, F. & L. VAN VALEN. 1974. Intellectual censorship in ecology. Ecology 55: 924–925.

POWELL, J. A. 1974. Occurrence of prolonged diapause in Ethmiid moths. Pan-Pac. Entomol. 50: 220–225.

ROTHSCHILD, M. & L. M. SCHOONHOVEN. 1977. Assessment of egg load by *Pieris brassicae* (Lepidoptera: Pieridae). Nature 266: 352–355.

SHAPIRO, A. M. 1981. The Pierid red-egg syndrome. Am. Nat., in press.
STEARNS, S. C. 1977. The evolution of life-history traits: a critique of the theory and a review of the data. Annu. Rev. Ecol. Syst. 8: 145–171.
THOMPSON, J. N. & P. W. PRICE. 1977. Plant plasticity, phenology, and herbivore dispersion: wild parsnip and the parsnip webworm. Ecology 58: 1112–1119.

NEW LOCALITY RECORDS FOR THE SALT MARSH COPPER, *EPIDEMIA DORCAS DOSPASSOSI* (LYCAENIDAE)

Since its discovery in 1939 (McDunnough, 1940, Canad. Ent. 72: 130–131) *Epidemia dorcas dospassosi* (McDunnough) has been recorded only from its type locality, Bathurst, New Brunswick (Ferris, 1977, Bull. Allyn Mus. 45: 1–42). In late July and early August 1979 I briefly searched every easily accessible salt marsh from Bartibog Bridge, Northumberland Co., New Brunswick to Campbellton, Restigouche Co., New Brunswick; and several salt marshes on the Gaspé Peninsula, Quebec, from Oak Bay on the Bay of Chaleur to Ste.-Anne des Monts on the south shore of the St. Lawrence River. *E. d. dospassosi* was collected in the following 9 localities, including 3 separate localities within the city limits of Bathurst.

1) Hay Island, 2 km south of Neguac, Northumberland Co., New Brunswick; 30 July 1979. 9 ♂ seen and collected, individuals were scarce and present only on the western tip of the island.

2) Wishart Point, mouth of Tabusintac River, Northumberland Co., New Brunswick; 31 July 1979. Adults numerous, 7 ♂ and 11 ♀ collected.

3) Village-des-Poirier, 4 km SW of Maisonnette, Caraquet Bay, Gloucester Co., New Brunswick; 2 August 1979. Adults scarce, 3 ♂ and 4 ♀ collected.

The following 3 localities are within the city limits of Bathurst, Gloucester Co., New Brunswick. These populations seem to be separated from each other by unsuitable habitat.

4) Carron Point, NE point of Bathurst Harbour; 1 August 1979. Adults very common in association with *Coenonympha nipisiquit* McDunnough.

5) East Bathurst, SE corner of Bathurst Harbour, mouth of Nepisiguit River; 28 July 1979. Adults very common.

6) Youghall Beach, NW corner of Bathurst, marsh bordering Peters River; 27 July 1979. Adults scarce, possibly just emerging, 3 ♂ and 1 ♀ collected, in association with *C. nipisiquit*.

7) Beresford, Gloucester Co., New Brunswick; 27–28 July 1979. Adults scarce, 5 ♂ and 8 ♀ collected. This locality is 5 km NW of Youghall Beach with a continuous salt marsh habitat between the two localities.

8) St.-Siméon, Bonaventure, Gaspé Peninsula, Quebec; 26 July 1979. A cool windy evening, 1 fresh ♂ collected resting on *Carex*.

9) Penouille, Gaspé, Gaspé Peninsula, Quebec; 24 July 1979. About 20 adults seen, 2 ♂ and 2 ♀ collected.

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TWO CALIFORNIA CHECKERSPOT BUTTERFLY SUBSPECIES: ONE NEW, ONE ON THE VERGE OF EXTINCTION

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ABSTRACT. The *Pedicularis*-feeding ecotype of *Euphydryas editha* occurring in the inner Coast Range to the east and south of San Francisco Bay, California, is described as a new subspecies, *E. e. luestherae*. The impact of the California drought of 1976–78 on the new subspecies was less severe than its impact on *E. e. bayensis*. In addition human activities have greatly reduced the amount of habitat suitable for *E. e. bayensis*. The combination has pushed *E. e. bayensis* close to extinction.

Lepidopterists have traditionally considered populations of *Euphydryas editha* (Boisduval) in the San Francisco Bay area to represent two subspecies, *E. e. baroni* Edwards to the north of the Bay, and *E. e. bayensis* Sternitsky on the San Francisco peninsula and in the inner Coast Range to the east and south.

The populations lumped in *E. e. bayensis*, however, represent two separate ecotypes (Ehrlich et al., 1975) which also are phenetically distinct. One set of populations occurs in islands of serpentine grassland in chaparral areas. The primary oviposition plant is the annual *Plantago erecta*, and *Orthocarpus densiflorus* serves as a key secondary foodplant, permitting larvae to survive to diapause size after the *Plantago* senesces. Populations are controlled in a largely density-independent manner by early spring rainfall and *Orthocarpus* abundance. Competition for larval food is absent. Adults are relatively sedentary since larval foodplants and adult nectar sources co-occur.

In contrast the other ecotype is dependent on *Pedicularis densiflora* for oviposition and larval development. Populations occur on slopes where the *Pedicularis* grows as a hemiparasite in the shade of shrubs. There are secondary foodplants (*Castilleja, Collinsia*), but none plays an important role in the dynamics of the *Euphydryas* populations. Regulation of population size is often density-dependent, with larvae starving in some years after *Pedicularis* plants are defoliated (White, 1974). Adults are more mobile than those of the *Plantago* ecotype, since nectar sources usually do not co-occur with the larval foodplant (Gilbert & Singer, 1973).

The two ecotypes responded differently to the California drought of 1976–78. The *Plantago* ecotype suffered more or less uniform declines; at least one and possibly several populations went extinct from the combined effects of drought and cattle grazing on their habitats. The surviving populations have been extremely slow in recovering. Some populations of the *Pedicularis* ecotype remained relatively un-

changed in size (Pozo, San Luis Obispo Co.), while others nearly disappeared (Del Puerto Canyon, Stanislaus Co.—DP). In contrast to the slow increase of populations of the *Plantago* ecotype since the return of normal rainfall, the Del Puerto Canyon population has increased very rapidly (Ehrlich, Murphy & Sherwood, in prep.).

The type locality of the Bay checkerspot, *E. editha bayensis*, was Hillsborough, California (Sternitsky, 1937), a location near EW on the map (Fig. 1). This name therefore is properly applied to the *Plantago* ecotype. The *Pedicularis* ecotype to the east and southeast of San Francisco is a new subspecies described below.

Euphydryas editha **luestherae** Murphy and Ehrlich, **new subspecies**
LuEsther's Checkerspot

Diagnosis. This new subspecies is phenetically distinguishable from *Euphydryas editha baroni* and *bayensis* by the overall lighter appearance of the dorsal aspect of the wings due to more extensive red and yellow scaling. Transverse rows of black, red and yellow are found on both dorsal and ventral wing surfaces. Along the outer margin of the upperside of the forewing is a narrow row of red spots bordered on the inside by black, then basad a row of yellow chevrons, then a wider band of black, then a row of yellow spots, followed again by a narrow band of black. The next band is red and is found approximately one-third the distance from the margin to the base of the wing in the postmedian region. Its color and extent is the key character for visually distinguishing this form from other northern California subspecies.

In *E. editha luestherae* this red band is very well developed, being much wider than those rows surrounding it; in some individuals, particularly females, the red band may be lightly suffused with yellow at basal and posterior margins. *Euphydryas editha baroni* and *bayensis* tend toward extreme reduction of this red band or heavy suffusion with, or replacement by, yellow scaling. In less than 2% of nearly 1000 individuals of subspecies *baroni* and *bayensis* before us is this central band of the forewing red and uninterrupted as in subspecies *luestherae*. Of 120 individuals of *luestherae* examined, 7 (5.9%) have interruptions in the diagnostic red band. In light of the great plasticity of wing phenotype within populations of this species, this may be considered a very strong diagnostic character.

A further distinguishing character is found on the venter of the forewing which in *Euphydryas editha luestherae* is heavily suffused with brick red across the basal two-thirds of the wing, disrupting the overall checkered appearance of the total underside characteristic of other North Coastal subspecies. This broad continuous area of red scaling is actually more similar to that found in coastal populations of *Euphydryas chalcedona* and is a particularly good character for discriminating *luestherae* from other *editha* subspecies in the Bay area, though less so in more southern locations.

We have found no consistent genitalic differences between the subspecies.

Types: Holotype ♂: California, Stanislaus Co., Del Puerto Canyon, 22 mi W of Patterson, 12 May 1973 (R. W. Garrison).

Allotype ♀: Same data. Types deposited in the American Museum of Natural History (AMNH).

Paratypes: 37 ♂♂ and 38 ♀♀. California: 2 ♀♀, Mt. Diablo, Contra Costa Co., 19 May 1951, T. W. Davies; 6 ♂♂ and 6 ♀♀, Mines Road, Alameda Co., 23, 27 April 1947, T. W. Davies; 25 ♂♂ and 24 ♀♀ Del Puerto Canyon, Stanislaus Co., various dates May 1971, 1973 and 1979, several collectors; 6 ♂♂ and 6 ♀♀ Pozo, San Luis Obispo Co., 7 May 1974, P. R. Ehrlich. Pairs of paratypes deposited at the California Academy of Sciences, and United States National Museum. The remainder of the type series is retained in the collection of the junior author at Stanford University. This collection will eventually be transferred to AMNH.
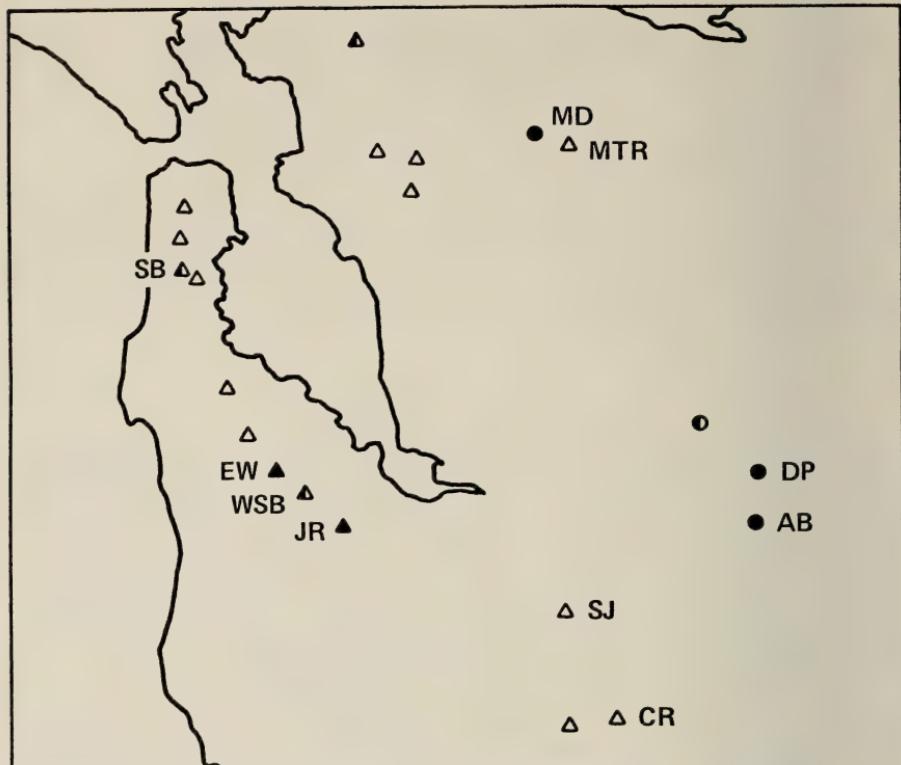
FIG. 1. San Francisco Bay area *Euphydryas editha*: populations with circles—ssp. *luestherae*; with triangles—ssp. *bayensis*. Filled symbols indicate extant colonies, half-filled indicate status unknown, and empty indicate known extinctions. Initials designate sites presently under active study by the Stanford group.

The holotype and allotype are taken from the well-known Del Puerto Canyon colony. Paratypes assigned include both the northern limit of this new taxon at Mt. Diablo, Contra Costa Co., California and the suspected southern limits at Pozo, San Luis Obispo Co., California. Colonies are additionally known from Alameda, San Benito and Monterey Counties, and others almost certainly remain undiscovered. *Pedicularis*-feeding populations in Napa and Sonoma Counties are phenetically intermediate to *baroni* and this new subspecies.

We are pleased to name this beautiful denizen of the Inner Coast Range after LuEsther, whose support of the work of our group on population problems and other factors that endanger butterflies and people has been invaluable.

The Threat to *E. e. bayensis*

Entire populations or large portions of habitat of *Euphydryas editha bayensis* have disappeared due to various causes including: 1) construction of a major freeway (Hillsborough, San Mateo, Edgewood—EW in part), 2) subdivision, construction, and introduction of

non-native plant species (Twin Peaks, Mt. Davidson, Brisbane, Joaquin Miller, San Leandro), and 3) the combined effects of drought and livestock grazing (Morgan Territory Road-MTR, Silver Creek—SJ, Coyote Reservoir—CR, Uvas Valley).

A single natural extinction followed by reestablishment and subsequent extinction was recorded in one of three small populations on Jasper Ridge Biological Preserve on Stanford University campus (Ehrlich et al., 1975).

In 1980 the status of two populations was doubtful. Several trips to San Bruno Mountain (SB) yielded no adults, and we fear that population may be extinct. And, towards the end of the flight season, massive construction operations destroyed most of the remaining habitat of the Woodside population (WS)—making its survival extremely doubtful.

It seems likely that populations of *E. e. bayensis* have always been subject to periodic extinctions from natural causes (weather fluctuations, fires) and were subsequently reestablished by migrants from other populations. In 21 years of work at Jasper Ridge, for example, we recorded a single transfer from the Woodside population 6.4 km away (Ehrlich et al., 1975). However, the number of islands of habitat suitable for this ecotype is now greatly reduced, and the distance between them increased. The Edgewood population is threatened by the development of a golf course, and over the long term it seems unlikely that Jasper Ridge alone can maintain the ecotype (an additional dry year in the last drought sequence might well have exterminated the two remaining populations there—Ehrlich et al., 1980). It should also be noted that while populations of the *Plantago* ecotype that go extinct may be recolonized by individuals from extant populations of the same ecotype, it is not possible on an ecological time scale for individuals from a different ecotype to repopulate vacated *Plantago* habitat. Thus *E. e. bayensis*, once extinct, cannot be reestablished by migration from *E. e. luestherae* populations (Gilbert & Singer, 1973). The two subspecies are clearly separate evolutionary entities.

The Bay Checkerspot is already an endangered butterfly. This sad situation is all the more distressing since its populations are among the best known—ecologically and genetically—of any invertebrate. We are attempting to get official protection for *E. e. bayensis* and are designing some experiments to recolonize areas of suitable habitat that are now vacant. We hope that all lepidopterists will leave the remaining colonies of *Plantago* ecotype undisturbed. All populations are being closely monitored, and those involved in reestablishment experiments will be especially vulnerable. We have dried specimens

taken in the past which we will make available on an exchange basis to collectors who do not have *E. editha bayensis* in their collections.

LITERATURE CITED

EHRLICH, P. R., R. R. WHITE, M. C. SINGER, S. W. MCKECHNIE & L. E. GILBERT. 1975. Checkerspot butterflies: a historical perspective. Science 188: 221–228.
EHRLICH, P. R., D. D. MURPHY, M. C. SINGER, C. B. SHERWOOD, R. R. WHITE & I. L. BROWN. 1980. Extinction, reduction and stability: the responses of checkerspot butterflies to the California drought. Oecologia (Berl.), 46: 101–105.
GILBERT, L. E. & M. C. SINGER. 1973. Dispersal and gene flow in a butterfly species. Am. Nat. 107: 58–73.
STERNITSKY, R. F. 1937. A race of *Euphydryas editha* Boisduval (Lepidoptera). Canad. Entomol. 69: 203–205.
WHITE, R. R. 1974. Foodplant defoliation and larval starvation of *Euphydryas editha*. Oecologia (Berl.) 14: 307–315.

GENERAL NOTES

NOTES ON THE NATURAL HISTORY OF *PAPILIO POLYXENES STABILIS* (PAPILIONIDAE) IN COSTA RICA

The black swallowtail butterfly *Papilio polyxenes* Fabr. occurs from southern Canada and the United States east of the Rocky Mountains through Mexico and Central America and into northern South America. Although the natural history of temperate populations has been well documented (e.g. Scudder 1889, The Butterflies of the Eastern United States and Canada with Special Reference to New England. Cambridge, Mass.; Clark, 1932, The Butterflies of the District of Columbia and Vicinity. U.S. Natl. Mus., Bull. 157; Rawlins & Lederhouse, 1978, J. Lepid. Soc. 32: 145–159), next to nothing is known about the species within its tropical range. As part of a comparative evolutionary study of temperate and tropical populations of the black swallowtail (Blau, 1978, A comparative study of the ecology, life histories, and resource utilization of temperate and tropical populations of the black swallowtail butterfly, *Papilio polyxenes* Fabr. Ph.D. diss., Cornell University; Blau, 1980, Ecology: in press), I spent ten months during 1976 near Turrialba, Costa Rica conducting experiments on the ecology of local populations. During these experiments, I noted many aspects of the natural history of the species, and those observations are summarized here.

The town of Turrialba is located on the Atlantic slope of the Cordillera Central of Costa Rica where the subspecies *P. polyxenes stabilis* Rothschild and Jordan is found. I studied localized colonies on the grounds of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), at about 600 m above sea level. Most of the land in this region is either cultivated for coffee and sugarcane or is used for pasture. The mean monthly temperature is nearly constant throughout the year at 22°C. The daily extremes average 5°C above and below the mean. The annual rainfall is approximately 2.6 m, with a dry season from January through April. (Meteorological data are from the weather station at CATIE.)

The black swallowtail probably occurs throughout Costa Rica wherever appropriate host plants are available. It has never been reported from the lowlands, but has been found at higher elevations up to about 1500 m. It has been sighted as far north as Monteverde (P. DeVries, D. Janzen, pers. comm.), as far south as San Vito (pers. obs.), and at many locations both on the Meseta Central and near Turrialba.

Approximately 22 species of Umbelliferae (the principal host plant family) occur in Costa Rica (Standley, 1938, Flora of Costa Rica. Field Mus. Nat. Hist., Chicago, Botanical Series, Publication 420; R. Rodriguez, pers. comm.), and perhaps 6 are potential hosts. Only 2 are known with certainty—*Apium leptophyllum* (Pers.) F. Muell (pers. obs.), and *Spananthe paniculata* Jacq. (obs. by D. Janzen, L. Gilbert; confirmed by P. Feeny). Both grow on the Meseta Central and are eaten by *P. polyxenes*, but the latter is the only common host plant in the Turrialba region. It is a broad-leaved forb which grows throughout the year from about 500–1500 m elevation. Occurring in moderate to severely disturbed sites, it is frequently a weed in sugarcane, coffee, and recently abandoned fields.

Favorable habitat for *P. polyxenes* is defined by the presence of the host plant. Because *S. paniculata* occurs early in succession, it is locally transient and grows in patches that vary greatly in size, condition and proximity to one another. The seeds germinate two weeks after a disturbance. About six weeks later, when the first small flowers are produced, the first ovipositions by *P. polyxenes* occur. The plants grow rapidly, flourish, and begin to senesce five or six months after germination.

The eggs of *P. polyxenes* are spherical, about 1 mm in diameter. They are laid singly on the flower or seed umbels (Fig. 1) and occasionally on the undersides of leaf edges of *S. paniculata*. They pass through a series of color changes—first all yellow, then yellow with a brown ring, turning completely brown, and then black—before hatching in 5–6 days.

The larvae are similar in appearance to those described from North America, with the exception that the dorsolateral rows of spots tend to be orange rather than lemon-

FIGS. 1–4.   **1,** *P. polyxenes* egg (arrow) on a developing seed of *S. paniculata*; **2,** green pupa of *P. polyxenes* on a blade of grass; **3,** fifth instar larva being attacked by an adult pentatomid bug; **4,** naturally mating pair of adults, female with wings spread.

colored (cf. Scudder, loc. cit.). During the first instar, larvae feed predominantly on flowers and young seeds. Later they feed on leaves as well, and by the end of the fifth (final) larval instar, they have grown to a length of 35–40 mm. Larval development is usually completed on a single plant, over 15–20 days. The larvae become quiescent for a short period before voiding the gut contents. They then wander in search of an appropriate pupation site which is usually within 2 m of the host plant (mean = 1.5 m, N = 5). After one-half to over two hours, a larva chooses a spot 10–50 cm (mean = 25 cm, N = 17) above the ground on a stem or other nearly vertical surface, and spins a silken pad to support the pupa. About a day later the final molt occurs, producing a pupa that may be green or brown depending on the characteristics of the substrate (Fig. 2) (West et al., 1972, J. N.Y. Entomol. Soc. 80: 205–211).

Most adults eclose after about two weeks, although some laboratory reared individuals have remained in the pupal stage for several months before eclosing. Prolonged pupal duration may be the result of gene exchange with populations of the Meseta

Central. There the dry season is more severe and appears to be passed in pupal diapause.

The larvae of *P. polyxenes* are attacked by several predators, including spiders, the wasp *Polistes canadensis costaricensis* Bequart, bugs in the families Reduviidae and Pentatomidae (Fig. 3), and probably ants. Members of the latter two groups also feed on pupae. Birds and lizards (genus *Ameiva*) are potential vertebrate predators. One parasitoid has been observed—a tachinid fly which attacks larvae and emerges as a prepupa during the host pupal stage. The rate of attack appears to be very low, however. Of 73 swallowtail pupae that were collected or followed in the field, only one produced tachinid prepupae. First and second instar larvae are also subject to drowning in water that accumulates on plant surfaces during prolonged periods of rain. The natural enemies of the adult stages are not known.

The adults of *P. polyxenes stabilis* possess a broader postmedian yellow band than the North American *P. polyxenes asterius*, and there is no sexual dimorphism in wing pattern (Fig. 4). Evidence from laboratory cultures and from the rate of wear of marked individuals in the field indicates that they survive for only three to four weeks. They commonly begin to fly by 0800, or when ambient temperatures reach about 23°C. Above this temperature flight occurs even under overcast conditions. Nectar feeding occurs on a variety of flowers, including *Emilia sonchifolia* (L.) DC. ex Wight, *Melanthera aspera* Jacq., and *Lantana* sp. A sample of 32 caged pupae yielded 18 adult males and 14 females. Although this ratio is not significantly different from unity (P = .49), new males were encountered three times more frequently than females over a two month period within one colony (N = 103), and seven times more frequently over a one month period within another (N = 23).

Male butterflies appear to patrol mating territories atop hills in a manner similar to New York males (Lederhouse, 1978, Territorial behavior and reproductive ecology of the black swallowtail butterfly, *Papilio polyxenes asterius* Stoll. Ph.D. diss., Cornell University). Under conditions of locally high population density, however, they exhibit a less aggressive "exploratory" flight away from hilltops. This flight is similar to that of an ovipositing female and may be an active search for newly eclosed, virgin females. Shapiro (1975, Am. Midl. Nat. 93: 424–433) notes a similar switch in the mate-locating behavior of pierid butterflies at high densities. In either case, males tend to remain in an area longer than females. Fifty-three percent of the individual males marked at one colony were later resighted at the same area (N = 75) compared with 21% of the females (N = 28). Among resighted individuals, the average male was last seen eight days after its first sighting (range 1–21 days) and the average female was last seen after three days (range 1–8 days). Females are likely to disperse in search of new host plant patches or to be chased away by aggressive and persistent males. This would account for their apparent paucity in the field.

Of nine field-caught females that were subsequently dissected, one contained two spermatophores, indicating that some females mate twice. Laboratory experiments indicate that the average female has the capacity to lay 436 ± 100 ($\bar{x} \pm s$) eggs (Blau, 1978, loc. cit.). The fertility of eggs laid in the field is about 90% (N = 50). Breeding populations were found throughout the ten months of this study, including the dry season, and almost certainly occur all year.

The natural history of *P. polyxenes* in Costa Rica differs in several ways from that of the north temperate subspecies, *P. polyxenes asterius*. The significance of differences in growth, reproduction, and host plant relationships have been studied and will be published elsewhere. Other questions merit further investigation. For example, what is the adaptive basis for variability in mate locating behavior in Costa Rica? What geographic patterns in diapause occur for *P. polyxenes* within the tropics, and what environmental cues, if any, are involved? How do geographic patterns in sexual dimorphism in *P. polyxenes* relate to the distribution of *Battus philenor* (L.), the model for the dark-form female?

Adult specimens of *P. polyxenes stabilis* from the population discussed here are located in the Cornell University Insect Collection, Lot 1023, Sublot 12 C.

The field studies in Turrialba would not have been possible without the cooperation

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REPEATED INTERGENERIC ATTRACTION BETWEEN INDIGENOUS AND
EUROPEAN SILKMOTHS (SATURNIIDAE)

Attraction of one species of saturniid by another in the same genus is well-known,
particularly with regard to the various members of *Hyalophora*, *Callosamia*, and *Sam-
ia*. Kershaw (1953, Ent. Rec. J. Var. 65: 219–220) reports an intergeneric attraction of
Phragmatobia fuliginosa L. males to a *Panaxia dominula* L. female, both British arc-
tiids. Dominick (1974, J. Lepid. Soc. 28: 176) even records an interfamilial attraction
involving *Amphion nessus* (Cramer) (Sphingidae) males and an *Anisota virginiensis
pellucida* (J. E. Smith) (Citheroniidae) female. However, the purpose of this note is to
record an intergeneric attraction between two saturniids which do not normally meet
in nature.

For several years I have been rearing *Saturnia pyri* Denis & Schiffermuller, from
France, for study purposes. Since these moths normally emerge during the first half of
May in this area, a time when most of our native saturniids are still in hibernation, I
was quite surprised to discover several large moths trying to gain entrance to our
screened porch on 8 May 1976, at 0130 EST. Upon allowing one to enter and discov-
ering that it was a male *Antheraea polyphemus* Cramer, I felt certain it would seek
out a female of the same species, which I had somehow failed to notice. Instead, it
flew directly to a transmitting female *pyri* and tried unsuccessfully to effect copulation.
Since that first experience, I have had numerous wild *polyphemus* males attracted to
other transmitting *pyri* females each year. The males are determined in their efforts
to mate and the females quietly submit to the incessant scratching and poking of the
males for as long as 20 min before one or the other breaks off contact. None of these
encounters has produced a successful union since the male *polyphemus* seems unable
to clasp the abdomen of the female *pyri*.

As the male *polyphemus* attempts copulation, the female *pyri* retracts her ovipositor,
making the end of her abdomen smooth with no protrusions on which to get a grip.
The male's abdomen repeatedly slides from side to side without being able to "lock
on." Visually, male *pyri* claspers appear to be larger than male *polyphemus* claspers.
It's possible that a male *pyri* may be able to clasp the last segment of the female's
abdomen and by applying pressure, force the female to extrude her ovipositor. The
male *polyphemus*, on the other hand, with smaller claspers and inability to grip the
female's abdomen, cannot apply pressure and mating attempts must necessarily fail.

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A CORRECTION OF THE NAME FOR THE TYPE-SPECIES OF *RHOPOBOTA* LEDERER (TORTRICIDAE: EUCOSMINI)

The genus *Rhopobota* Lederer, 1859, was described to include *Tortrix naevana* Hübner [1814–1817], a species known in North America as the black-headed fireworm. Subsequently, *Tortrix unipunctana* Haworth, 1811, was recognized as a senior synonym of *Tortrix naevana* (Bradley et al., 1972, *In* Kloet & Hincks, A checklist of British insects, second ed., part 2, Lepidoptera. R. Entomol. Soc. Lond.; Karlsholt & Schmidt Nielsen, 1976, Systematisk fortegnelse over Danmarks sommerfugle. Scand. Science Pr., Klampenborg, Denmark). In a recent paper on nomenclatorial changes in Eucosmini (Brown, 1979, J. Lepid. Soc. 33: 21–28), I also listed *Tortrix unipunctana* Haworth as the senior name for the type-species of *Rhopobota*. I have been recently informed by Dr. John Bradley, of the Commonwealth Institute of Entomology, London, that *Tortrix unipunctana* Haworth is a primary homonym of *Tortrix unipunctana* Donovan, 1805 (Epitome of Natural History of Insects of New Holland, Pl. 40). This homonomy has been obscured by the misspelling of *unipunctana* Donovan as *unipunctata* in the Index Animalium (Sherborn, 1931, British Museum (Natural History), London). As *unipunctana* Haworth is the junior homonym, the next available name for the type-species of *Rhopobota* is *Tortrix naevana* Hübner, the name historically used in North America.

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OBITUARY

BRISBANE CHARLES SOMERVILLE WARREN (1887–1979)

B.C.S. Warren of Folkestone, England, died on 22 January 1979. His most notable contribution (among many) was his *Monograph of the genus Erebia,* published by the British Museum (N.H.) in 1936. He spent four years carrying out the needed research, and in writing this definitive volume. In 1944, he started a short series of papers devoted to the classification of the Argynnidi. For me, his most interesting studies relate to the androconial scales of pierids. These brought about the revision of several perplexingly similar species.

A brief note concerning his early introduction to entomology and a bibliography of his 112 papers was published by Warren in Nota Lepid. 1(2): 77–81, 31 March 1978. An obituary and photograph of him appeared in the Entomologist's Record, 1979 in the April issue, pp. 111–112.

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BOOK REVIEW

A REVISION OF THE GENUS *HIPPARCHIA* FABRICIUS, by Otakar Kudrna. 1977. E. W. Classey, Ltd., Faringdon, Oxon., England. 300 pp., 353 figs., 1 plate (frontispiece). Price £19.00 (approximately $41.00 U.S.).

This revision formed the basis of Kudrna's Master of Philosophy dissertation submitted in 1977 to Portsmouth Polytechnic. In many ways it reads like a Master's thesis, but it is also a workmanlike taxonomic revision of a very difficult genus. The revision was not hampered by any lack of material, and Kudrna is to be congratulated for searching out and examining so many of the type specimens.

The descriptions of the various taxa are lucid and detailed, but some of Kudrna's remarks upon them are rather sophomoric, especially the comments upon species that have several subspecies. Here I point to the rather shallow treatment in the discussion of *H. autonoe* (Esper) on p. 45, as an example. The section on "Taxonomic Considerations" (pp. 170–175) is rather well thought out, albeit perhaps briefer than it should have been; this section does demonstrate that Kudrna is a competent systematist. His "Zoogeographical Considerations" (pp. 176–180), however, are much too brief and demonstrate a certain lack of understanding and "feel" for the subject. That section is basically a descriptive one of the ranges of species and extracted information about Palearctic faunal types, but the interrelationships between the geographical ranges of the species of *Hipparchia* (and any possible derivations of them) are not elucidated.

The illustrations of the butterflies and their genitalia are well done and show what they are supposed to show. I suspect that these genitalic photographs could have been reduced by one half without losing clarity. One plate, carrying Figs. 126–127, lacks a caption (p. 240) for the figures of the genitalia of *H. p. pellucida* (Stauder) and *H. p. cypriensis* (Holik). This, presumably, is an oversight of the publisher.

The text matter is printed by photolithography from typed camera-ready pages on uncoated paper. One must wonder whether it will last indefinitely. The plates, by contrast, are printed on a glossy, somewhat heavier paper that gives a greater impression of permanence. The quality of the paper, and the fact that the text is not typeset, is not what one would expect to obtain in a book of this size that costs more than $40.00, and I am rather disappointed in the production of it.

This book, objections notwithstanding, is a must for the satyrid taxonomist with any interest in this fascinating genus. Readers with Palearctic affinities will probably want to have it in their libraries. But I cannot recommend it to the reader who is looking for general truths or who does not have an abiding interest in the Palearctic satyrids. The book is just too expensive for the "meat" it delivers. Read it in your museum or university library instead.

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NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of the collection and study of Lepidoptera. Contributors should prepare manuscripts according to the following instructions.

Abstract: A brief abstract should precede the text of all articles.

Text: Manuscripts should be submitted in *triplicate*, and must be typewritten, *entirely double-spaced*, employing wide margins, on one side only of white, 8½ × 11 inch paper. Titles should be explicit and descriptive of the article's content, including the family name of the subject, but must be kept as short as possible. The first mention of a plant or animal in the text should include the *full scientific name*, with *authors* of zoological names. Insect measurements should be given in *metric units*; times should be given in terms of the *24-hour clock* (e.g. 0930, not 9:30 AM). Underline only where *italics* are intended. References to footnotes should be numbered consecutively, and the footnotes typed on a separate sheet.

Literature Cited: References in the text of articles should be given as, Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and all must be listed alphabetically under the heading Literature Cited, in the following format:

Sheppard, P. M. 1959. Natural selection and heredity. 2nd. ed. Hutchinson, London. 209 p.

——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10: 165–216.

In the case of general notes, references should be given in the text as, Sheppard (1961, Adv. Genet. 10: 165–216) or (Sheppard 1961, Sym. R. Entomol. Soc. London 1: 23–30).

Illustrations: All photographs and drawings should be mounted on stiff, *white* backing, arranged in the desired format, allowing (with particular regard to lettering) for reduction to their final width (usually 4½ inches). Illustrations larger than 8½ × 11 inches are not acceptable and should be reduced photographically to that size or smaller. The author's name, figure numbers as cited in the text, and an indication of the article's title should be printed *on the back* of each mounted plate. Figures, both line drawings and halftones (photographs), should be numbered consecutively in Arabic numerals. The term "plate" should not be employed. *Figure legends* must be typewritten, double-spaced, *on a separate sheet* (not attached to the illustrations), headed Explanation of Figures, with a separate paragraph devoted to each page of illustrations.

Tables: Tables should be numbered consecutively in Arabic numerals. Headings for tables should not be capitalized. Tabular material should be kept to a minimum and must be typed *on separate sheets*, and placed following the main text, with the approximate desired position indicated in the text. Vertical rules should be avoided.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes at this time will be charged to authors at the rate of 75ᵉ per line. A purchase order for *reprints* will accompany the proofs.

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CONTENTS

JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

Michael Parsons

THE LEPIDOPTERISTS' SOCIETY

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The object of the Lepidopterists' Society, which was formed in May, 1947 and formally constituted in December, 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

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Cover illustration: Mature larva of *Ornithoptera goliath* Oberthür eating through the thick, corky stem of *Aristolochia crassinervia*, consuming the higher concentrations of secondary plant compounds that the stem of this vine contains. Original drawing by Mr. Michael J. Parsons, F.R.E.S., Hurst Lodge, Hurst Lane, Egham, Surrey TW20 8QJ, England.

THE LIFE HISTORY OF *AELLOPOS TANTALUS*
(SPHINGIDAE)

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ABSTRACT. The life history and immature stages of *Aellopos tantalus* are described for the first time. The larval host plant is seven year apple, *Casasia clusiifolia*, a member of the coffee family, Rubiaceae. Larvae exhibit a green or a brown color phase in the fourth or fifth instar. Pupation occurs in the leaf litter with adults emerging in the morning. In the Florida Keys, *tantalus* appears to have a minimum of 6 generations per year. Adults were usually observed shortly before and after sunrise, and again prior to dusk.

Aellopos tantalus (L.) is a small sphingid of tropical origin, which occurs with a great deal of regularity in the Florida Keys. The adults in this genus are characterized by their small size, dark coloration, and the presence of a white band on the terga of the fourth abdominal segment. Hodges (1971) pointed out that the host plant and immature stages of *tantalus* are unknown. While living in the Florida Keys, I had the opportunity to rear the larvae of this species, and make observations on the adults. This paper describes the larval stages and biology of *A. tantalus*.

First instar. **Head:** Green; diameter 0.6 mm. Clypeus green. **Body:** Length 7.5 mm, width 1.3 mm. Ground color green. True legs green. Prolegs green. Spiracles green. Anal horn black, length 2.2 mm. Anal shield with two brown lines extending from posterior area at base of horn to anal shield.

Second instar. **Head:** Green; diameter 1.5 mm. **Body:** Length 11.5 mm, width 1.9 mm. Coloration identical to first instar. Anal horn length 3.5 mm.

Third instar. **Head:** Green; diameter 2.2 mm. Clypeus green. **Body:** Length 16–18 mm, diameter 3.4 mm. Ground color green. Diagonal yellow lines on abdominal segments, extending from base of prolegs dorsally, terminating in the subdorsal intersegmental area of the adjacent posterior segment. Prominent yellow line extending from base of prolegs on abdominal segment VI, and terminating at base of anal horn. True legs, green. Prolegs, green. Spiracles, green. Anal horn length, 4.6 mm, red at base, mid portion green, tip brown.

Fourth instar. (Fig. 1). **Head:** Diameter 3.3 mm. **Body:** Length 21–23 mm, width 4.6 mm. **Coloration:** If ground color is green, the head, clypeus, prolegs, and ventral

surface are green. Anal horn blue-green. If ground color is brown, the head, clypeus, prolegs, and ventral surface are brown, and the anal horn is black. Patterns and colors common to both color forms: diagonal yellow-orange lines on lateral surface of all abdominal segments as in third instar. Diagonal cream-colored lines originating on dorsal surface of abdominal segment II, and at base of horn are very prominent, and at least twice the diameter of diagonal yellow-orange lines. Dorsal area whitish, with white paniculum. Subdorsal area between yellow-orange lines, orange with pinaculum of this area also orange. Faint subdorsal longitudinal orange line extending from first thoracic segment to prominent diagonal line on abdominal segment II. Anterior dorsal area of prothoracic segment with orange or white band next to head. Spiracles, gray or orange. Yellow lines extending from base of anal horn to anal shield. Anal shield same as ground color but with trace of violet near base. Anal horn, straight, length, 5.2–5.5 mm.

Fifth instar. Head: Diameter 5.5 mm. **Body:** Length 49–51 mm, width 9.4 mm. Anal horn 4.5 mm long, and posteriorly curved. As in the fourth instar, the larvae exhibit two color forms, one green, the other brown. There is no noticeable difference between fourth and fifth instar larvae, other than overall size and the shape and length of the anal horn.

DISCUSSION

Adult *A. tantalus* have a rapid flight, making them difficult to capture except when they nectar. Though *tantalus* is said to be a dayflier, the majority of adults were observed shortly before and after sunrise, and again prior to dusk, with few sightings during the rest of the day. On Plantation Key, most adults were observed nectaring at the blooms of white stopper, *Eugenia axillaris* (SW.), with a few individuals visiting flowers of lantana. Adults were found in clearings, or around the periphery of hardwood hammocks, but not within the hammock.

Female *tantalus* were observed ovipositing on seven year apple, *Casasia clusiifolia* Urban, in the late afternoon. In older literature this plant is referred to as *Genipa clusiaefolia* Jacq. *Casasia* is native to south Florida and a member of the coffee family, Rubiaceae. Once the host plant was known, I found that almost every plant examined supported eggs, larvae, or showed signs of feeding damage. Thus, though the adults were never overly abundant, the immature stages were exceedingly common. The eggs are light green and round, measuring 1.4 mm in diameter, and are laid singly on the new tender growth of the host plant. At ambient temperatures in July (31°C high, 28°C low) the eggs hatch in 2.5 days. During the first three instars all individuals are green, but upon molting into the fourth or fifth instar, the ground color may change from green to brown. Fig. 1 illustrates a brown phase, fourth instar larva. Similar changes occur in the larvae of *A. fadus* (Cramer) and *A. titan* (Cramer), and were illustrated by Moss (1920).

Early instar larvae were found feeding only on the new growth. While last instar larvae also preferred new growth, they were fre-
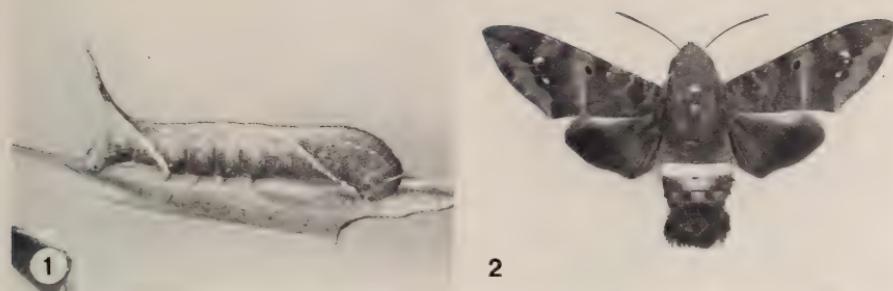
FIGS. 1–2. **1,** brown color phase of fourth instar larva; **2,** ♀ *A. tantalus.*

quently found on fully formed leaves that were not yet mature. Considering the distribution of this moth in Florida, other plants besides *clusiifolia* must serve as larval hosts. Empty egg shells and feeding damage similar to that of *tantalus* were found on pond apple (*Annona glabra* L.) but no larvae were observed. In captivity *tantalus* larvae consumed the tender leaves of *A. glabra* and were able to complete development.

As the mature larva prepares to pupate, its color changes from green or brown to dark red. The pupation chamber is constructed under a few inches of leaf litter and is formed by spinning just enough silk to hold the surrounding debris together. During the summer, 26 days are required for development from the egg to the emergence of the adult. As temperatures cool during January and February, the low temperatures slow the development of larvae and pupae, and adults are uncommon. Although cool temperatures greatly increase the length of time in the pupal stage, no diapause was observed. Thus, *tantalus* appears to have a minimum of 6 generations a year in the Florida Keys. Adults, which emerge in the morning, have a dark green cast to the dorsal surface, and a wide range of subtle colors which are lacking in individuals more than a day old (Fig. 2).

LITERATURE CITED

HODGES, R. W. 1971. The moths of America north of Mexico. Fascicle 21, Sphingoidae. Classey, London. 1–158 pp.
MOSS, A. M. 1920. Sphingidae of Para, Brazil. Novit. Zool. 27: 333–424.

EFFECTS OF LONG AND SHORT DAY PHOTOPERIODS ON THE SEASONAL DIMORPHISM OF *ANAEA ANDRIA* (NYMPHALIDAE) FROM CENTRAL MISSOURI[1]

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ABSTRACT. Larvae of the goatweed butterfly, *Anaea andria* Scudder, when reared at 27°C produce summer form adults under a long day (16L:8D) photoperiod, and winter form adults under a short day (12L:12D) photoperiod. Adults from the progeny of both the summer and winter forms exhibit this response and evidence is given to support the premise that the fifth instar larva is the stage in which adult form is determined.

The length of the daily photoperiod has been shown to be an important factor in regulating the appearance of several butterfly species. Müller (1955, 1956), Müller & Reinhardt (1969) and Reinhardt (1969, 1971) have shown that in *Arashnia levana* L. (Nymphalidae) the seasonal dimorphism is primarily controlled by photoperiodic exposure during the larval stage, with temperature modifying this effect under certain conditions. Hidaka & Aida (1963) and Hidaka & Takahashi (1967) have shown that larvae of *Polygonia c-aureum* L. (a Japanese nymphalid) reared at 20°–26°C under 14 or more hours of light produced characteristic "summer form" adults, while a photoperiod of 12 or less hours produced "winter forms," and a 13 h light period produced adults of both forms with no intermediates. They also demonstrated that extreme temperatures could override the photoperiod induced effects. Additional studies by Ae (1957), Shapiro (1968), Oliver (1970) and Shapiro (1973) using the respective pierid butterflies, *Colias eurytheme* Boisduval, *Pieris protodice* Boisduval and LeConte, *P. napi oleracea* Harris and *P. occidentalis* Reakirt, and Sakai & Masake (1965) using the lycaenid, *Lycaena phlaeas daimio* Seitz, have also shown that the photoperiodic exposure of the immature stages is a major factor in the regulation of seasonal dimorphism in these species. Dimorphism is expressed principally as differences in color in the pierids, and as differences in color as well as in wing shape in *L. p. daimio*.

The goatweed butterfly, *Anaea andria* Scudder, exhibits pronounced seasonal dimorphism in the wing shape of both sexes. Individuals of the summer brood (summer forms) are characterized by
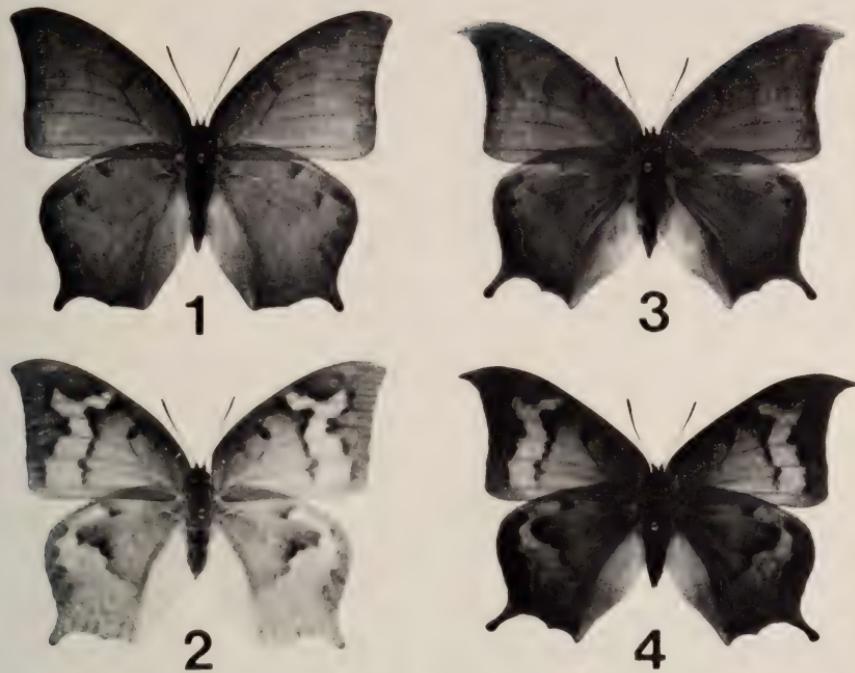
FIGS. 1–4. *Anaea andria* Scudder. **1,** ♂ summer form; **2,** ♀ summer form; **3,** ♂ winter form; **4,** ♀ winter form.

a blunt forewing apex, short, stubby tails and a reduced anal projection on the hind wing (Figs. 1 & 2). Adults emerging in the fall (winter forms) are characterized by having forewing apices developed into a slightly recurved, falcate projection, tails with a slightly expanded tip and a well-developed projection at the anal angle of the hind wings (Figs. 3 & 4). The color of adult *A. andria* males is red-orange above with a dark brown margin to the wings. Winter form males typically have a wider marginal band. In most summer form males, the dark scaling of the forewing margin is reduced and appears completely absent in some specimens. On the hind wings of both forms the dark margin originates at the anterior of the outer wing margin and continues to the anal angle. The winter forms typically exhibit a broader, darker continuous hindwing band, while in summer forms the band is narrow and penetrated by the red-orange color along the veins. In females the color of the wings above is tan to orange and paler than in the males. The dark marginal band is present to approximately the

same degree on both wings in both forms, as are several dark markings in the submarginal area of the wings. The under side of each sex of both forms is cryptically colored in gray-brown. Winter forms are usually darker and mostly brown in color, while summer forms are lighter with a predominance of gray colored scales. Fresh examples of both forms exhibit a slight silvery sheen. Generally, the winter form butterflies are darker and richer in color than the summer forms, with males possessing a wider dark marginal band on the upper side of the forewings. Variation is found in both forms and a large series of each will show a range in the intensity of the red-orange color as well as in the width of the marginal band.

Winter form individuals are so designated because they emerge in the fall and overwinter as adults. In central Missouri they can be collected from late August throughout the winter months on warm days, until May or early June the following year. Successful mating of these overwintering individuals occurs in the spring. Summer form butterflies are the progeny of the overwintered adults and in central Missouri they are present from late June through August, with stragglers present on into September. These individuals mate and oviposit within a short time of emergence, and their offspring then become winter form individuals. There are, then, in central Missouri two broods of *A. andria*: one in which the adults live for as many as 9 or 10 months (winter forms); and one in which the adults survive for only 1 or 2 months (summer forms). The winter form is the form described and figured by Edwards (1868) as *Paphia glycerium,* and the summer form was formally described by Johnson & Comstock (1941).

The host plants for *A. andria* in central Missouri are *Croton capitatus* Michx. (goatweed or woolly croton) and *Croton monanthogynus* Michx.

The experiments reported here were designed to determine the effect rearing larvae of *A. andria* under a short day (12L:12D) or long day (16L:8D) photoperiod at 27°C on the seasonal form of the adults; to examine whether photoperiodically induced effects were produced in adults reared from larvae of both summer and winter form adults; and to elucidate when during development the adult form is determined.

METHODS AND MATERIALS

Eggs and larvae were collected in the field on their host plants and brought into the laboratory for rearing. Eggs were first observed on 29 May 1978; at this time the *Croton* plants were at the two leaf stage and 5.0–7.5 cm tall. The last collection of larvae was made on 12 Sept.

1978, when first through fifth instars were collected. Immatures were collected in early and late summer to obtain progeny of both the overwintered winter forms and their summer form offspring. Two pupae (collected 17 and 24 Aug. 1978), were also kept under a 16L:8D photoperiod until emergence of the adult.

Eggs and larvae were placed in clear plastic boxes measuring 30 × 15 × 9 cm for rearing. The boxes contained a raised 3 mm mesh grid platform on which fresh leaves, eggs and larvae were placed. A paper towel covered the bottom of the box and facilitated cleaning of the containers. The boxes were covered with unvented clear plastic tops (to keep moisture relatively high and constant). They were placed in one of two environmental growth chambers, both chambers kept at 27°C, one with a 12L:12D (short day) regime and the other with a 16L:8D (long day) regime.

The length of the photoperiods was chosen to represent the shortest and the longest daylengths to which larvae would be exposed in central Missouri. The shortest daily photoperiod would be 11 h 58 min on 1 October, from sunrise to sunset with no dawn or dusk twilight period. The longest daily photoperiod would be 15 h 55 min on 18 June including a 30 min civil twilight period at dawn and dusk. These data were obtained from the Department of Meteorology at the University of Missouri-Columbia, and from Beck (1968).

Two groups of larvae were also kept in clear plastic containers near windows where they were exposed to the natural daylength. The first group consisted of 16 eggs and first instars collected 19 June 1978. The second group contained 18 fourth and fifth instars and 6 chrysalids collected 31 Aug. 1978 and 7 fifth instars collected 12 Sept. 1978.

Larvae were fed fresh leaves of *Croton monoanthogynus* daily. This plant was chosen as food because it was the most common local species of *Croton*. Prior studies with *A. andria* have shown that larvae feed readily on either *C. monanthogynus* or *C. capitatus* no matter which plant they were feeding on when collected.

RESULTS AND DISCUSSION

Tables 1 and 2 summarize the results obtained by rearing larvae of *A. andria* under a short day photoperiod or under a long day photoperiod. The adults obtained from the eggs and larvae collected 19 June and reared under natural light as controls were all summer forms with blunt wing apices; those obtained from the larvae collected 31 August and 12 September and reared under natural light as controls were all winter forms with falcate wing apices. The adults obtained from the two chrysalids collected 17 and 24 August and kept under long day photoperiod were both winter form individuals.

Table 1. Summary of adult forms of *Anaea andria* obtained from immatures reared at 27°C under long and short day photoperiods.

Date collected and immature stage	12L:12D		Date collected and immature stage	16L:8D	
	Sum-mer	Win-ter		Sum-mer	Win-ter
May 30 egg	0	4	May 30 egg	3	0
May 30 1st instar	0	4	June 19 egg	7	0
June 4　egg	0	7	June 19 2nd instar	1	0
June 19 egg	0	9	Aug. 6　egg	18	0
June 19 2nd instar	0	12	Aug. 6　1st instar	7	0
Aug. 6　egg	0	11	Aug. 6　2nd instar	9	0
Aug. 6　1st instar	0	7	Aug. 6　3rd instar	8	0
Aug. 6　2nd instar	0	15	Aug. 6　4th instar	7	0
Aug. 6　3rd instar	0	2	Aug. 6　5th instar	5	0
Aug. 6　4th instar	0	7	Aug. 17 5th instar[1]	32	9
Aug. 6　5th instar	0	4	Aug. 27 5th instar[1]	0	6
Aug. 27 5th instar	0	6	Aug. 31 5th instar[1]	6	3
			Sept. 12 1st–4th instars	33	0
Total	0	88		129	18
Percent	0.0	100		87.8	12.2

[1] See Table 2.

Tables 1 and 2 show that at 27°C the length of the photophase to which larvae of *A. andria* are exposed affects the adult form. Eggs collected 30 May, 4 June and 19 June 1978 were assumed to have been deposited by females of the overwintering population, since in 1978 winter form individuals were quite common at this time of year and the two species of host plants had just begun to sprout during the last week of May. In nature, these eggs and larvae would have developed into summer form individuals with blunt wing apices, as did the 16 larvae reared under natural light as controls. If photoperiod had no effect, this result would be expected in laboratory reared individuals. Table 1 shows that, when reared under a short day photoperiod, all of the adults from these eggs were of the winter form with falcate wing tips. Adults obtained from larvae collected as eggs on 30 May and reared under a long day photoperiod were of the expected summer form with blunt wing apices.

The eggs and larvae collected in August and September were presumed to be from summer form adults as blunt winged specimens were then on the wing and had been for some time. In the natural environment these immatures would be expected to develop into winter form individuals with falcate wing apices, as did the larvae collected 31 August and 12 September and reared as controls under natural light. If photoperiod were not influential, they would be expected to develop into winter form adults under laboratory conditions

TABLE 2. Percentage of winter form *Anaea andria* and time between pupation and collection as 5th instar larvae (when reared under long day photoperiod at 27°C).[1]

Days between collection and pupation	Larvae pupated	% Winter form adults
2	6	100.0
3	9	100.0
4	9	11.1
5	19	10.5
6	6	0.0
7	2	0.0
8	3	0.0
9	1	0.0
10	0	0.0
11	2	0.0
12	0	0.0
13	0	0.0
14	1	0.0

[1] Larvae collected on 17, 27, and 31 August.

as well. However, when reared under long day photoperiod, 87.8% of the adults obtained were of summer form; 12.2% were winter form. No intermediate forms were obtained.

An explanation for the 12.2% winter form individuals is suggested by comparing the time between collection as fifth instar larvae and pupation for winter form butterflies with the same time span for the resulting summer form individuals (Table 2). All the larvae that became winter form adults pupated within 5 days of the date on which they were collected. This suggests that the factor(s) determining the form of the adults had already been programmed, and that the insects could no longer be influenced (as fifth instar larvae or as pupae), by daylength when subjected to a long day photoperiod in the laboratory. That the other fifth instar larvae developed into summer form adults when subjected to long day photoperiod suggests that the length of the photoperiod determines the form of the adult in the fifth instar up to approximately five days prior to pupation.

The two pupae kept under long day photoperiod both produced winter form individuals. One of these required 11 days from the time of collection to the emergence of the adult; the other required 10 days. The time between pupation and emergence of 50 *A. andria* reared under a long day photoperiod was 7 to 11 days, so it can be assumed that these two pupae were collected soon after they pupated in the field and were therefore exposed to the long day photoperiod throughout almost the entire pupal stadium. If photoperiod had an effect on these insects in the pupal stage, one would expect these to produce summer form individuals, although the natural photoperiod

could have had an effect on the first days after pupation. Two specimens is too small a sample to draw conclusions. However, in the group of fifth instar larvae discussed above (those taken from the natural, short day conditions of late August and mid-September and placed in a long day photoperiod), the first larvae to pupate produced adults of the winter form one would expect under natural conditions, despite being exposed to the long day photoperiod during the first days after pupation. Those pupating later produced summer forms. These data indicate that the fifth instar larva and not the pupa is the stage in which adult form is determined.

The time required for development (from egg collection to adult emergence, at 27°C) was 4–5 weeks. For the summer forms, developmental time was 25–42 days (mean = 32.2 days). For the winter forms, developmental time was 27–50 days (mean = 37.3 days). Larvae from the summer form adults therefore would be expected to reach the fifth instar in central Missouri from mid-August until the first hard frosts of fall. The length of the natural photoperiod (from sunrise to sunset) from 15 August to 1 October in Columbia is 13 h 43 min, decreasing to 11 h 58 min, corresponding roughly to the short day (12L:12D) photoperiod. The larvae from the overwintering winter form adults would be expected to reach the fifth instar from mid- or late June through late July. The hours of natural daylight from sunrise to sunset for 1 June to 31 July in Columbia range from 14 h 43 min to 13 h 47 min, with maximum at 18 June (14 h 55 min); or if 30 min dawn and dusk twilight periods are included, 15 h 55 min. Larvae developing during these months would then be doing so under the longest days of the year, corresponding roughly to the long day (16L:8D) photoperiod.

I tentatively conclude that in central Missouri it is the length of photoperiod to which fifth instar larvae are exposed, until approximately 4–5 days prior to pupation, that is a major factor determining the seasonal form of adult *A. andria*. That seasonal wing dimorphism occurs in other species of *Anaea* is well documented by Comstock (1961). When discussing *A. aidea*, Comstock (1961) refers to the blunt winged form as the summer or dry season form; and in their discussion of *A. aidea aidea* and *A. aidea floridalis*, Johnson & Comstock (1941) also refer to the summer forms as dry season forms and to the winter forms as wet season forms. These references to wet and dry seasonal forms suggest that wing shape in these species is influenced by the seasonal moisture of their native habitat. No experimental evidence substantiates this idea in *Anaea* and no mention is made of the possible role of photoperiod. The data presented in this paper suggest

that photoperiod exerts influence on determination of seasonal forms in species of *Anaea* in addition to *A. andria*.

ACKNOWLEDGMENTS

LITERATURE CITED

AE, S. A. 1957. Effects of photoperiod on *Colias eurytheme*. Lepid. News 11: 207–214.

BECK, S. D. 1968. Insect photoperiodism. Academic Press, New York. 288 pp.

COMSTOCK, W. P. 1961. Butterflies of the American Tropics. The genus *Anaea*, Lepidoptera, Nymphalidae. Amer. Mus. Natl. Hist., New York. 214 pp.

DANILEVSKII, A. S. 1965. Photoperiodism and seasonal development of insects. Robert Cunningham & Sons Ltd., Alva. 283 pp.

EDWARDS, W. H. 1868. The Butterflies of North America. Vol. 1. Houghton Mifflin, Boston.

HIDAKA, T. & S. AIDA. 1963. Daylength as the main factor of seasonal form determination in *Polygonia c-aureum* (Lepidoptera, Nymphalidae). Zool. Mag. 72: 77–83.

HIDAKA, T. & H. TAKAHASHI. 1967. Temperature and maternal effect as modifying factors in the photoperiodic control of the seasonal form in *Polygonia c-aureum* (Lepidoptera, Nymphalidae). Annotationes Zool. Jap. 40: 200–204.

JOHNSON, F. & W. P. COMSTOCK. 1941. *Anaea* of the antilles and their continental relationships with descriptions of new species, subspecies and forms (Lepidoptera, Rhopalocera, Nymphalidae). J. New York Entomol. Soc. 49: 301–343.

MÜLLER, H. J. 1955. Die Saisonformbildung von *Araschnia levana*, ein photoperiodisch gesteurter Diapause-Effekt. Naturwiss. 43: 134–135.

——— 1956. Die Wirkung vesschiedener diurnaler Licht-Dunkel-Relationen auf die Saisonformbildung von *Araschnia levana*. Naturwiss. 43: 503–504.

MÜLLER, H. J. & R. REINHARDT. 1969. Die Bedeutung von Temperatur und Tageslänge für die Entwicklung der Saisonformen von *Araschnia levana* L. Lepidoptera. Nymphalidae). Entomol. Berichte 1969: 93–100.

OLIVER, C. G. 1970. The environmental regulation of seasonal dimorphism in *Pieris napi oleracea* (Pieridae). J. Lepid. Soc. 24: 77–81.

REINHARDT, R. 1969. Uber den Einfluss der Temperatur auf den Saison-dimorphismus von *Araschnia levana* L. (Lepidopt. Nymphalidae) nach photoperiodischer Diapause-Induktion. Zool. Jahrb. Physiol. 75: 41–75.

——— 1971. Modifizierung der Photoperiodisch bedingten Saisonformen von *Araschnia levana* L. durch Temperaturveränderugen. (Abstract). Limnologica 8: 538.

SAKAI, T. & S. MASAKI. 1965. Photoperiod as a factor causing seasonal forms in *Lycaena phlaeas daimio* Seitz (Lepidoptera: Lycaenidae). Kontyu 33: 275–283.

SHAPIRO, A. M. 1968. Photoperiodic induction of vernal phenotype in *Pieris protodice* Boisduval and LeConte (Lepidoptera: Pieridae). Wasmann J. Biol. 26: 137–149.

——— 1973. Photoperiodic control of seasonal polyphenism in *Pieris occidentalis* Reakirt (Lepidoptera: Pieridae). Wasmann J. Biol. 31: 291–299.

A NEW SPECIES OF THE GENUS *PEORIA* RAGONOT (PYRALIDAE)

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ABSTRACT.   This paper includes a description of the new North American species *Peoria padreella.*

Peoria padreella A. Blanchard, **new species**

Description.   Frons with conical tuft of pale grayish luteous scales; labial palpi porrect, three times as long as eye diameter, basal segment pale luteous, second and third segments grayish luteous, paler beneath; maxillary palpi reaching apex of frontal tuft. Antennae luteous; pubescence about as long as shaft diameter in male, finely ciliate in female. Occiput, vertex, patagia, tegulae and dorsum of thorax shiny luteous; legs pale luteous.

Forewing (Fig. 1).   Reddish luteous, the reddish tint more noticeable in frontal half along basal two thirds of costa; irregularly sprinkled with blackish scales, more heavily in distal fourth and at base of fringe. Fringe somewhat paler than ground color, without black scales.

Hindwing (Fig. 1).   Paler luteous than forewing, without reddish tint nor black scales; fringes concolorous.

Length of forewing.   Males 6.1 and 6.7 mm, female 6.3 mm.

Venation.   Forewing, R_2 stalked with R_{3+5}, the stalk as long as the free part of R_2; M_1 free, M_2 absent, M_3 very shortly stalked with Cu 1; Cu 2 from near lower outer angle of cell; discocellular vein extremely weak. Hindwing, R_s stalked with Sc+R, the stalk about as long as the free part of Sc+R; M_{2+3} completely fused with Cu 1; Cu 2 from near lower outer angle of cell; only the ends of the discocellular vein are visible.

Male genitalia (Figs. 2, 3 & 3a).   The slide of Fig. 2 (A.B. 3758) was prepared in the conventional manner; it is somewhat distorted. The slide of Figs. 3 and 3a (Knudson slide) was prepared following the procedure used by J. C. Shaffer (1968, pages 3 and 4). The paired lateral spicate processes of the uncus have only one well developed arm instead of two like all other species of the genus, but the missing arm is indicated by a short blunt knob. The gnathos is thin, weakly sclerotized and without an apical spicate process; it is much widened in its middle. The juxta missing in Fig. 3 is quite obvious in Fig. 2. The vesica of the aedeagus (Fig. 3a) is unarmed. Valves with simple costa.

Female genitalia (Fig. 4, from slide A.B. 4607). Bursa thinly membranous, without signum; ductus seminalis from small pointed diverticulum near junction to ductus bursae; ductus bursae short in its narrow part, becoming as wide as about two fifths the diameter of eighth segment at its ostial end; ostial chamber about as long as wide.

Types.   Holotype: ♂, Padre Island National Seashore, Kleberg Co., Texas, 24 June 1976, collected by A. & M. E. Blanchard, deposited in the National Museum of Natural History, type No. 76140. Paratypes: Padre Island National Seashore, Kleberg Co., Texas, 30 Sept. 1975, 13 Oct. 1979, ♀ ♀ collected by A. & M. E. Blanchard. North Padre Island, Nueces Co., Texas, 1 Oct. 1977, ♂ collected by E. C. Knudson.

Remarks.   *Peoria padreella* differs from all other species of the genus in having one-arm spicate processes of the uncus (instead of the usual two-arm ones). The southeastern *Peoria roseitinctella* (Ragonot), the Brazilian *P. punctilineella* (Hampson) (see Shaffer 1976a, p. 301) and *P. punctata* Shaffer (1976b) appear to be the only other species of the genus with six-vein hindwings.

Table I (Shaffer, 1968, p. 12) compares 12 sets of characters for the known North American species of *Peoria*. For *P. padreella* the symbols O, *, O, O, O, O, O, p, x, ss, O, O may be added in columns 1 through 12 of that table.
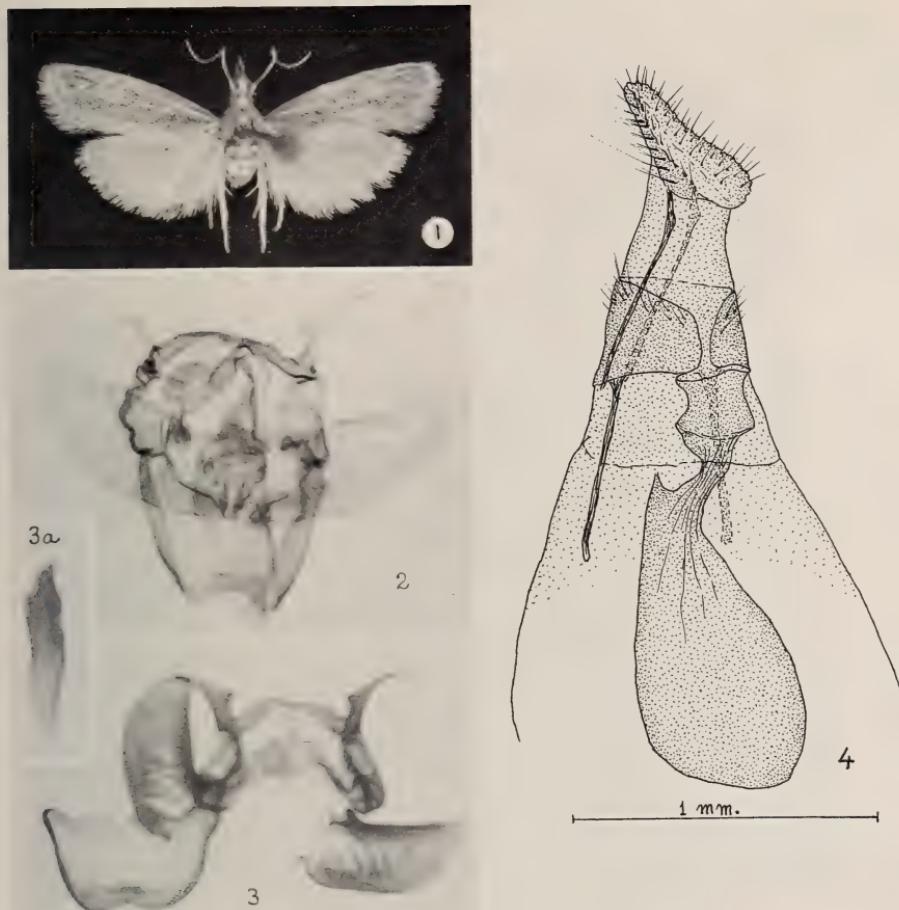
FIGS. 1–4. *Peoria padreella*. **1**, ♂ holotype; **2**, genitalia of holotype. **3**, ♂ genitalia of paratype (Knudson slide); **3a**, aedeagus. **4**, ♀ genitalia of paratype.

LITERATURE CITED

SHAFFER, J. C. 1968. A revision of the Peoriinae and Anerastiinae (Auctorum) of America North of Mexico. U.S. Natl. Mus. Bull. 280. 124 pp.

—— 1976a. A revision of the Neotropical Peoriinae. Syst. Entomol. 1: 281–331.

—— 1976b. Two new species of Peoriinae (Lepidoptera: Pyralidae) from Texas. Proc. Entomol. Soc. Washington 78: 434.

BILATERAL GYNANDROMORPHIC *SPEYERIA DIANA* (NYMPHALIDAE)

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ABSTRACT. Laboratory reared and field collected bilateral gynandromorphs of *Speyeria diana* are described. Comparisons are made with normal siblings of the laboratory reared gynandromorph and with normal specimens collected with the field caught gynandromorph. Development time of the laboratory reared gynandromorph was intermediate between those of normal male and female siblings. This may be linked with the fact that the male sides of both gynandromorphs were disproportionately large while the female sides were small.

A bilateral gynandromorph of the Diana Fritillary, *Speyeria diana* (Cramer), was reared by Showalter during September and October, 1973. This butterfly was one of 23 adults that developed from eggs obtained from a female taken 19 August 1973 in Poverty Hollow, Montgomery Co., Virginia. Initiation of larval feeding was induced by a method similar to that described by Mattoon, Davis, and Spencer (1971) and the larvae began feeding over a three-day period. Rearing temperature was 24°C. Adult emergence dates indicate that development time of the gynandromorph was intermediate between the development times of male and female siblings. Adult males emerged 2–7 days earlier than the gynandromorph (4.2 ± 1.38 days earlier [x̄ ± s]). The females emerged 2–7 days later than the gynandromorph (4.0 ± 1.79 days later). Pupation dates were not recorded but males generally pupated before females.

The gynandromorph appears to be perfectly bilateral with the right side male and the left side female. The color pattern of each side is normal compared to other *S. diana* specimens (Figs. 1 & 2). Externally, the genitalia are bilaterally asymmetrical with a misshapen clasper on the male side. The right eye (male) is larger than the left, measuring 3.4 mm dorsoventrally. The left eye measures 2.8 mm. The conical spines on the dorsal side of the pupa differ in shape (Fig. 3). The right spines are blunt like those of normal males and the left ones are more pointed like those of females.

An interesting fact about this butterfly is that the male side is larger than average for males; the female side is smaller than average for
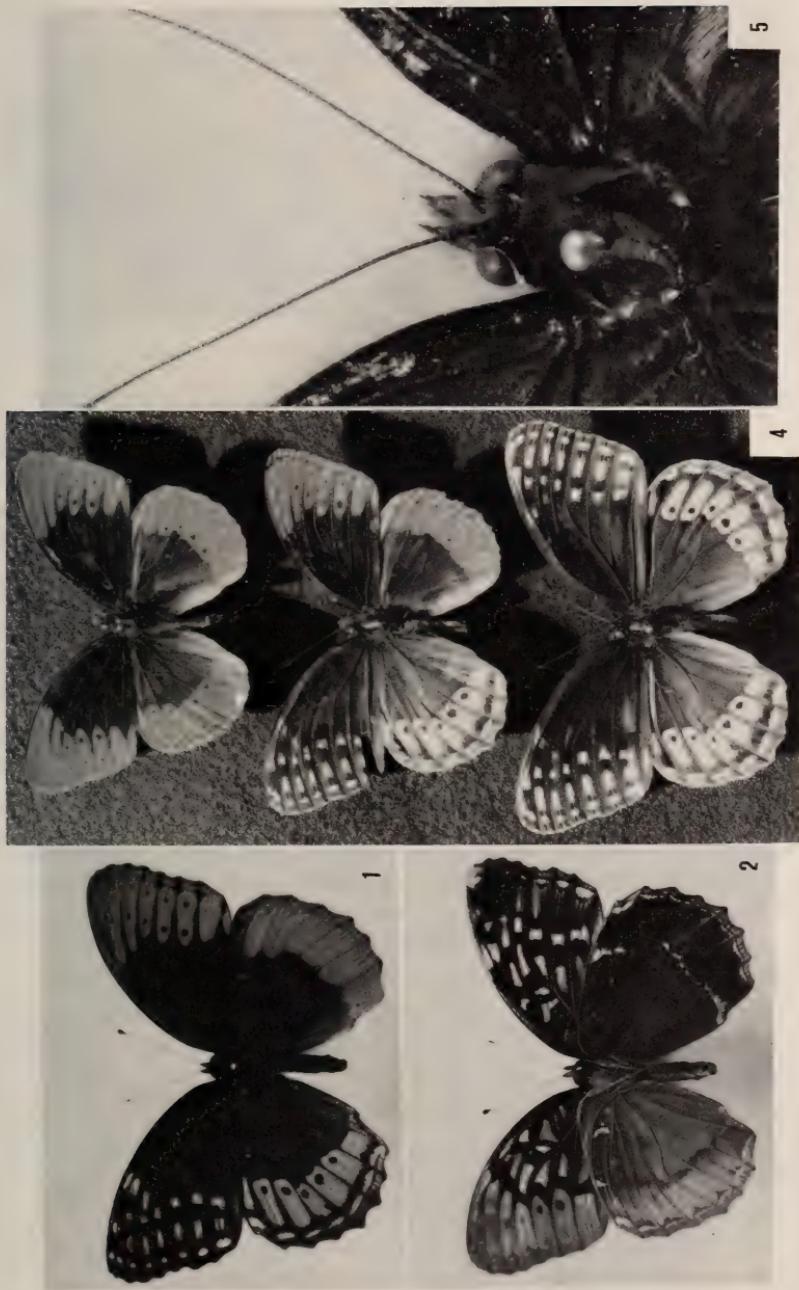
FIGS. 1, 2, 4, 5. *Speyeria diana* gynandromorphs and normal individuals. **1**, laboratory reared *S. diana* gynandromorph, upper side; **2**, laboratory reared *S. diana* gynandromorph, under side; **4**, field caught *S. diana* (from top), ♂, ♀, and gynandromorph (photograph by Glenn Berkey); **5**, close-up of field caught gynandromorph *S. diana* (photograph by Glenn Berkey).

Fig. 3.   Laboratory reared *S. diana* gynandromorph, pupa.

females. The male forewing is 48 mm long and the female forewing is 51 mm long. Clark & Clark (1951) say that the forewing lengths of male *S. diana* normally range from 43 to 47 mm while those of females range from 50 to 55 mm. Forewing lengths of siblings are given in Table 1 for comparison. The male side of the pupa was larger than the female side (Fig. 3). Normal male pupae are smaller than female pupae.

Thomas Allen of the West Virginia Department of Natural Resources field collected a bilateral gynandromorph *S. diana* near Pinnacle Creek, Wyoming Co., West Virginia on 12 July 1978 (Fig. 4). The seasonal range for *S. diana* in West Virginia extends from 13 June to 2 August. The gynandromorph, together with normal male and female specimens collected at the same time and location, was measured and photographed. Table 1 presents the largest diameter or length of the eye and wing radius measurements and the ratio of wing to eye lengths obtained from the three West Virginia specimens.

The laboratory reared gynandromorph and the slightly smaller field collected specimen are strikingly similar. Size variations between the two gynandromorphs were probably influenced by differing environmental factors such as temperature, humidity and availability of food. Eye and wing measurements of the field collected gynandromorph are only slightly larger than normal for the male half, while the female side is much smaller than normal. In both specimens, the left half is female with normal markings, and the right half is male and possesses male genitalic structures. The male sides feature modified pale setae along the costal margins of the dorsal surfaces of the hindwings which may be scent scales or androconia (Fig. 5). Unlike the male hindwing of the laboratory reared specimen, the field

TABLE 1. Eye and wing measurements and wing:eye ratios of laboratory reared and field collected *Speyeria diana*.

	Eye length (mm)	Wing radius (mm)	Wing:eye ratio
Reared specimens			
Males	—	44.9 ± 1.2(16)[1]	—
Females	—	54.0 ± 2.2(5) [1]	—
Gynandromorph			
Male half	3.4	48	14.1
Female half	2.8	51	18.2
Field collected specimens			
Male	3.1	44.1	14.2
Female	3.1	52.3	16.9
Gynandromorph			
Male half	3.2	45.2	14.1
Female half	2.7	47.8	17.7

[1] Mean values ± standard deviation (numbers in parentheses = sample size).

collected gynandromorph has the normal double row of rounded brown spots along the orange band of the dorsal wing surface, and the left front wing has a chip on cell Cu_2. Results in Table 1 indicate that normal male and female specimens from West Virginia fall within the range of wing sizes obtained from laboratory reared specimens. The ratios of wing to eye measurements are fairly consistent between normal and gynandromorph specimens.

The female sides of both gynandromorphs are smaller than those of normal females, and the male sides are either equal to or larger than normal male specimens. Rearing data shows that males eclose approximately 8 days before females. If it is also true that males pupate earlier than females and that gynandromorph pupation occurs at an intermediate time, then these size differences are not surprising and could be due to the length of the larval feeding period. What triggers the behavioral change from that of feeding to that of seeking a pupation site is not known, but probably has a genetically controlled endocrinological basis modified by environmental conditions. The physiological relationships between the two sides of the gynandromorphs are not known, and thus we are unable to conclude from the available evidence how these developmental factors caused the disproportionate dimensions in the strikingly dimorphic *Speyeria diana* gynandromorphs.

ACKNOWLEDGMENTS

LITERATURE CITED

CLARK, A. H. & L. F. CLARK. 1951. The butterflies of Virginia. Smithsonian Misc. Coll. 116(7), 227 pp., 30 pls.

MATTOON, S. O., R. D. DAVIS & O. D. SPENCER. 1971. Rearing techniques for species of *Speyeria* (Nymphalidae). J. Lepid. Soc. 25: 247–256.

SOME ASPECTS OF THE BIOLOGY OF THE DEVELOPMENTAL STAGES OF *COLIAS ALEXANDRA* (PIERIDAE)

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ABSTRACT. Aspects of the larval ecology and behavior of *Colias alexandra* Edw., a pierid native to the Rocky Mountains, are described here. The study populations are univoltine (although bivoltine pockets exist) and monophagous, utilizing *Lathyrus leucanthus* Rydb. as a larval host plant. A high degree of specificity is exhibited by ovipositing females. Pre- and postdiapause feeding activity is described. Diapause occurs in the third instar; photoperiod and temperature are suspected as cues. Parasitoid and hyperparasite interactions are described, including a previously undescribed species of *Gelis* (Ichneumonidae). *Colias alexandra* occurs with several other species of *Colias*. Adult food sources are shared and, in one case, there is ecological overlap of the developmental stages.

In recent years agriculturally important members of the genus *Colias* have been among the most intensively studied and best known Lepidoptera. In comparison, relatively little is known about the biology of the developmental stages of other *Colias* species. This article summarizes observations made during four years of study on the larval ecology and behavior of *Colias alexandra* Edwards.

Colias alexandra, first described by Edwards in 1873, is native to the Rocky Mountains and occurs from New Mexico, northward to Alberta, westward to Nevada and British Columbia (Brown et al., 1957). Adults fly from late June to early August throughout montane meadows from approximately 1800 m to timberline. Univoltine and bivoltine populations exist, although univoltinism is predominant.

Study Sites and Methods

Observations on larval biology were made while monitoring a permanent demography plot (20 m × 20 m) from 1975 to 1978, along Brush Creek, 13 km SE of Crested Butte (Gunnison Co.), Colorado (2950 m). Relatively large populations of *C. alexandra* occur in this area (Watt, et al., 1977). They are univoltine and utilize *Lathyrus leucanthus* Rydb., a legume, as a larval foodplant. The vegetation within the plot is representative of this fescue grassland (see Langenheim, 1962) and was searched thoroughly (on hands and knees) for

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C. alexandra eggs and larvae. Plants with eggs or larvae were marked with flags. The behavior, developmental rates and mortality of the larvae were then recorded on a regular basis throughout the season. Additionally, ovipositing females were followed to observe host seeking and oviposition behavior (Stanton, 1975).

RESULTS AND DISCUSSION

Oviposition and Foodplant Choice

Females exhibit a high degree of specificity in oviposition. A single egg is deposited on the surface (usually abaxial) of the leaf of *L. leucanthus* (Fig. 1) with nearly 100 percent accuracy, although in the Brush Creek population, rare mistakes have been observed on *Agoseris glauca* (Pursh) Dietr. (Compositae). Other mistakes occur on two legume species, *Lupinus* sp. and *Vicia americana* Muhl, which are often found side by side with the host plant and which I find nearly indistinguishable from *L. leucanthus* when both are immature. Attempts to rear larvae on alternative native plants have proven successful in a few cases (*Lupinus* sp., *Trifolium longipes* and *Vicia americana*), but growth rates are slower (D. Henneberger, pers. comm., pers. obs.). Thus, while other host plants are known for *C. alexandra* (Ellis, 1973), members of a single population appear to be monophagous.

Multiple oviposition on a plant (i.e., more than one female ovipositing on a plant) is relatively rare (<10%, N = 1000), although females do not appear to scan the leaves visually as do *Heliconius* (Alexander, 1961; Gilbert, 1975), searching for eggs. On two occasions a single small plant (<10 cm in height, 12 leaves) was found with 5 *C. alexandra* eggs. The number of eggs per plant resembles a Poisson distribution, i.e., selection of a foodplant for oviposition appears to be a random process. No instance of multiple occupation of the same plant has resulted in multiple larval survival. Larvae of all instars react to disturbance by "rearing," a sudden upward movement of the head and first several segments, and are more easily dislodged during this activity. As a result, encounters with conspecifics may cause one or both to drop from the plant (pers. obs.). Also, cannibalistic habits of the larvae of this genus have been observed (J. Grula, pers. comm.) and have been found occasionally in lab colonies of *C. alexandra* (pers. obs.) when food is in short supply.

Prediapause Larval Behavior

Eggs are white when oviposited and turn pink (characteristic of the genus) within 48 hours if fertile. The mean egg development time in

FIGS. 1–4. *Colias alexandra* prediapause stages. **1**, egg on *Lathyrus leucanthus* leaf; **2**, second instar larva feeding on *L. leucanthus* in characteristic manner leaving vascular tissue intact; **3**, just-molted third instar; **4**, diapausing third instar larva.

the field, oviposition to hatching, is 11 days (Table 1). At hatching, the egg shell is at least partially consumed by the larva. Feeding on a leaf begins with the chewing of a small hole on the surface. This behavior results in characteristic "pinholes" and has been observed for other species of *Colias*, e.g., *eurytheme* (Sherman & Watt, 1973), *philodice* and *meadii* (pers. obs.). Occasionally more than one pinhole is initiated. Once feeding has begun the larvae assumes a cryptic green coloration characteristic of the genus (Gerould, 1922; Sherman

Table 1. A timetable for *Colias alexandra* developing in the field (13 km SE of Crested Butte, Colorado, elev. 2950 m). This table summarizes data gathered in 1977 and 1978.

Stage	1977			1978		
	Mean	S.D.	N	Mean	S.D.	N
Egg (oviposition–hatching)	11.02	0.72	97	11.34	0.77	73
1st instar (hatching–1st molt)	9.22	0.86	90	8.89	0.76	82
2nd instar (1st–2nd molt)	12.24	1.6	50	9.99	0.97	54
3rd instar (2nd–diapause)	6.51	0.91	29	8.11	1.10	31
Diapause						
3rd instar (diapause–3rd molt)	2.41	0.73	7	3.09	0.81	6
4th instar (3rd–4th molt)	6.01	0.95	7	5.77	1.21	6
5th instar (4th–5th molt)	4.86	1.19	4	5.37	0.93	5
Pupa (pupation–eclosion)	12.73	1.62	3	14.12	1.56	3

& Watt, 1973). The head remains black until the first molt. Mean development time in the field from hatching to first molt is 9 days (Table 1).

As it develops, the larva begins to enlarge one of its original pin-holes. Most feeding is done from a position on the midrib of the leaf. A fine "network" of vascular tissue from the ventral side of the leaf is left behind as feeding continues (Fig. 2). From late first through third instars larval feeding produces these networks. On a mature leaf, networks are maintained between the midrib and the border of the leaf. The leaf remains turgid as the larva avoids the tougher vascular portions of the leaf. Feeding, in general, is restricted to the distal two-thirds of the leaf, although immature leaves as well as tendrils may be totally consumed by second and third instar larvae.

Movement of early instars is minimal, involving moving along the midrib between feeding and resting—a distance of half to the entire length of the leaf (1–2 cm). Movement to a new leaf or branch occurs in conjunction with molting (Fig. 3); however, even after moving, larvae often return to previously occupied sites to feed. First instar larvae rarely leave the site of their first network. By late third instar, a larva may have left a dozen or more networked leaves, having travelled to two or three branches, but having never left the plant on which the egg was placed by the female. Exceptions occur when the tops of two or more foodplants are in contact, in which case the larva may wander to another plant.

After a feeding period, the larvae move down the midrib toward the stem to begin a resting phase. The position of the resting larva relative to the leaf is a highly specific character. First through third instar

larvae assume a position on the midrib, head "stemward," on the distal third of the leaf. Each successive instar positions itself in closer proximity to the stem. This resting position is frequently not visible from above due to the overlapping position of the leaves on each branch. This behavior has been observed in other legume feeding *Colias*, e.g., *eurytheme* (Sherman & Watt, 1973; Hayes, 1975) and *philodice eriphyle* (pers. obs.). It is possible that this position is simply a good location to avoid incidental disturbance which may result in dislodgement from the plant. Should a larva become dislodged, the result is probably fatal. On the ground, the larvae are susceptible to predation by a variety of ground inhabitants, especially spiders and ants (pers. obs.), and desiccation (Strauss, 1978). The resting position may also be a microclimate adaptation (Waterhouse, 1960), as the overlapping leaves and branches produce a shading effect which is maximally effective closest to the stem. This behavior may serve as an avoidance mechanism from visual predators (e.g., Gerould, 1922) or parasitoids. Two hymenopterous parasitoids have been reared from fifth instar larvae (Figs. 5 and 6): *Apanteles flavicornis* (Ichneumonidae) which also was obtained from *C. philodice eriphyle* larvae and *Nepiera* sp. (Brachonidae). Additionally, a new species of *Gelis*, a hyperparasite (Ichneumonidae), has been reared from *A. flavicornis* which emerged from *C. alexandra*.

Diapause

Late third instar larvae cease feeding activities and move to an untouched leaf or to a neighboring plant (Fig. 4). These larvae are sluggish, appear somewhat swollen and lighter green in color with a darkened head capsule which is small relative to the body. *C. alexandra* overwinter as a diapausing third instar larvae. The cues for the initiation of diapause in *C. alexandra* have not been determined although photoperiod and temperature are jointly suspected (Ae, 1958; Hayes, unpubl. data). Diapausing individuals either remain on the plant and eventually are buried in the leaf litter when the plant falls or they crawl down the stem to the base and enter the litter to overwinter. The litter and snow cover very likely buffer the larvae from the extremes of winter.

The factor(s) responsible for diapause termination are as yet unknown, but increased daylength and ground temperature are believed to play roles in the resumption of activity. Synchrony of emergence of the larvae with the new growth of the larval foodplant is critical. The larval host plant, *L. leucanthus*, emerges in the spring at different times throughout the population range, thus a flexible diapause terminating cue would be advantageous. In fact, larval diapause may be

FIGS. 5–8. *Colias alexandra* postdiapause stages. **5,** parasitized fifth instar larva; **6,** pupae of *Apanteles flavicornis* reared from fifth instar larva; **7,** fifth instar larva; **8,** pupa.

an adaptation to avoid mature and less nutritious growth late in the growing season.

Postdiapause Larval Behavior

After emerging from diapause the postdiapause larvae begin to feed at once and the third molt occurs soon after activity resumes. The

fourth and fifth instar larvae are more mobile than young larvae, larvae of each instar foraging over approximately a one square meter area. Larvae may initiate feeding with the characteristic networking, but rapidly progress to consuming all the leaf material. Often whole leaves are consumed and tender new plants may be reduced to a piece of stem before a larva moves on. Larvae feed from a position on the leaf or stem. The mean field development time of the later instars, third to fourth molt is 6 days and fourth to fifth molt is 5 days (Table 1).

During resting phases these larger larvae retreat to the stem. The later instars have distinct lateral stripes which mimic highlights on the plant stem (Fig. 7), as do other *Colias* (Sherman & Watt, 1973). Again the resting position may serve as a predator or parasitoid avoidance mechanism, represent a microclimate selection adaptation or provide a secure footing for the immobile larvae. At the cessation of feeding the fifth instar larvae position themselves among the leaves of a host plant or sage or within a dense clump of grass as the pupation process begins. Characteristic of the genus, the new pupa is a solid green which changes within a few hours to display lighter lines that mimic leaf highlights as it dries and hardens (Fig. 8). The mean field development time of the pupa, pupation to emergence, is 14 days.

Interactions with Congeners

C. alexandra is the "middle" of three species of *Colias* whose often overlapping habitats lie along an elevational gradient in this area of the Rocky Mountains. *C. philodice eriphyle* is found from the high plains to 2700 m and *C. meadii* occupies the alpine zone above timberline. Also present in this area is the non-legume (*Salix*, Salicaceae) feeding *C. scudderi* and the frequent migrant from lower elevations, *C. eurytheme.*

C. alexandra interactions with *C. meadii* are minimal since their breeding areas are often separated by forest. There are occasionally years when *C. eurytheme* migrates in large numbers into this area from New Mexico, but its interactions with resident species are unknown. It does successfully utilize *L. leucanthus* as a larval foodplant (Hayes, unpubl. data). *C. scudderi* and *alexandra* do not share the same family of larval host plant, but often share adult nectar sources with *C. eurytheme* and *p. eriphyle* during the overlapping flight periods (Watt et al., 1974). Generally, nectar resources do not appear to be limiting in this region. The preferred larval foodplants of *C. p. eriphyle* are *Vicia americana* and *Trifolium* spp. (Stanton, unpubl. data). Under some conditions, such as low soil moisture conditions in 1977, *C. p. eriphyle* will utilize *L. leucanthus* for oviposition in sig-

nificant numbers during one or both broods (Hayes, unpubl. data). Additionally, the parasitoid, *A. flavicornis* has been reared from *C. p. eriphyle* and may utilize *alexandra* and *p. eriphyle* as alternative hosts, although the exact relationship is unknown.

Literature Cited

Ae, S. A. 1958. Comparative studies of developmental rates, hibernation and food-plants in N. American *Colias* (Lep., Pieridae). Amer. Midl. Nat. 60: 84–96.

Alexander, A. J. 1961. A study of the biology of the caterpillars, pupae and emerging butterflies of the subfamily Heliconiinae in Trinidad, West Indies. I. Some aspects of the larval behavior. Zoologica 46: 1–24.

Brown, F. M., D. Eff & G. Rotger. 1957. Colorado Butterflies. Denver, Denver Museum of Natural History. 368 pp.

Edwards, W. H. 1873. Butterflies of N. America. vol. I. Supplementary Notes. Amer. Entomol. Soc. Philadelphia. 215 pp.

Ellis, S. L. 1973. Field observations on *C. alexandra* Edwards (Pieridae). J. Lep. Soc. 28: 114–124.

Gerould, J. H. 1921. Blue-green caterpillars: origin and ecology of a mutation in the haemolymph color in *Colias philodice*. J. Exp. Zool. 34: 385–414.

Gilbert, L. E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. Pp. 210–240 *in* L. E. Gilbert and P. H. Raven, eds. Coevolution of Animals and Plants. Austin, Univ. Texas Press.

Hayes, J. L. 1975. Orientation behavior of *Colias eurytheme* larvae: the midrib resting position of early instars. Honors Thesis, Stanford Univ., Stanford, California.

Langenheim, J. H. 1962. Vegetation and environmental patterns in the Crested Butte Area, Gunnison County, Colorado. Ecol. Monogr. 32: 249–285.

Sherman, P. & W. B. Watt. 1973. The thermal ecology of some *Colias* butterfly larvae. J. Comp. Physiol. 83: 25–40.

Stanton, M. L. 1975. The mechanisms and evolutionary origins of oviposition specificity in *Colias* butterflies. Honors Thesis, Stanford Univ., Stanford, California.

Waterhouse, F. L. 1960. The microclimatic zones near leaves and twigs and postural behavior of a geometrid larva. XI. Inter. Cong. Ent. 689–693.

Watt, W. B., P. C. Hoch & S. G. Mills. 1974. Nectar resources used by *Colias* butterflies. Oecologia 14: 353–374.

Watt, W. B., F. S. Chew, L. R. G. Snyder, A. G. Watt & D. E. Rothchild. 1978. Population structure of pierid butterflies. I. Densities and movements of three montane *Colias* species. Oecologia 27: 1–22.

INTER-PEAK DISPERSAL IN ALPINE CHECKERSPOT BUTTERFLIES (NYMPHALIDAE)

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ABSTRACT. Inter-peak transfer was demonstrated for the first time in butterflies. Dispersal rates were lower for females than for males. Dispersal—as measured by velocity per day, distance moved between recaptures, and net range of individuals—was greater from more sparsely populated, less favorable areas.

In spite of field work during the past ten years (e.g., Scott, 1975; Brussard & Ehrlich, 1970; Gilbert & Singer, 1973; Watt et al., 1977; Watanabe, 1978) there remain many important questions about the vagility of butterflies in natural populations. Much of the work done involved very localized areas, small colonies of animals, or both. The remainder of the data involve larger areas, but suffer from various defects, especially inadequate coverage of the study area (e.g., Schrier et al., 1976).

In the former case local demographic units have been identified and dispersal within them has been characterized. A demographic or ecological population is a local concentration of individuals that may be counted in a demographic sense, and which is the essential unit of ecological impact in terms of resource utilization or carrying capacity. These units have independent dynamic behaviors. They may or may not be independent genetic units (demes). This assertion can rarely be made regarding migration between such colonies. This is unfortunate because the reproductively successful transfer of only a few individuals can, under some circumstances, meld two colonies into one Mendelian population (McKechnie et al., 1975; Ehrlich & White, 1980; Lewontin, 1974).

It is partly for logistical reasons that few studies of larger areas have been done. It is far more difficult to observe dispersal between than within demographic units. In studies of larger areas a few workers have shown that demographic units exchange significant numbers of individuals (Watanabe, 1978; Watt et al., 1977; Brussard & Ehrlich, 1970; Ehrlich & Gilbert, 1973). Thus the Mendelian populations defined by gene flow may contain several distinct demographic units.

Individuals of most species are far from uniformly distributed in space. This may be due to obviously discontinuous resource distributions or to less obvious factors. Whenever organisms occur in apparently discrete units, questions about inter-colony vagility arise. In the case of such a distribution the question of whether there are nu-
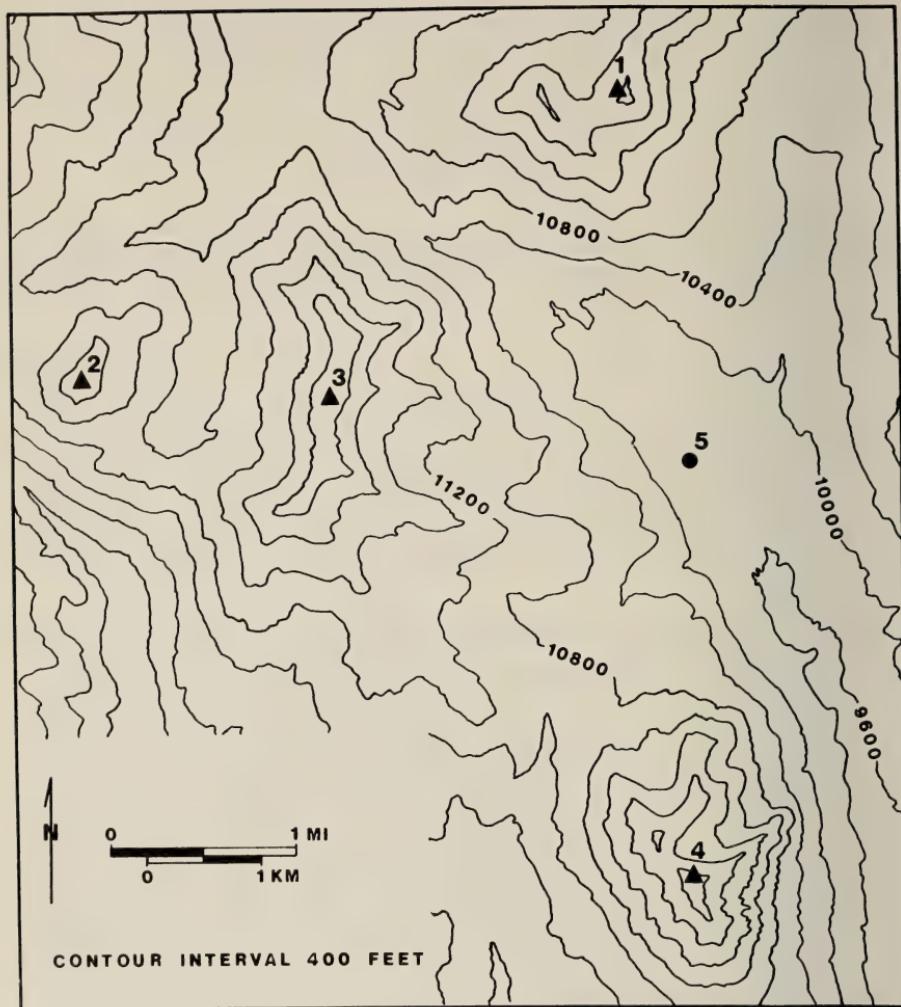
FIG. 1.   Contour map of study area. **1,** Bellview; **2,** Cinnamon; **3,** Mt. Baldy; **4,** Gothic; **5,** release-point on road at 9700 ft, equidistant from the peaks of 1, 3, and 4.

merous, separately evolving populations or a single evolving species can be answered only with vagility (realized dispersal) data which allow assessment of the magnitude of gene flow (Ehrlich & Raven, 1969).

MATERIALS AND METHODS

To determine the structure of high altitude checkerspot butterfly populations four colonies of *Euphydras anicia* (Doubleday) were selected for study. *E. anicia* is found throughout Colorado at both high

and low elevations. Populations occurring in alpine zones are sometimes given the subspecific name *eurytion* (Mead), and seem to form a distinct group within the species (Brown et al., 1957; Howe, 1975). Alpine populations of the species occur from New Mexico northward to Wyoming and Montana.

The four colonies selected occupied the alpine zones of the following peaks (Fig. 1) in Gunnison Co., Colorado: Cinnamon Mt., 12,300 ft (3747 m); Mt. Baldy, 12,800 ft (3900 m); Bellview Mt., 12,500 ft (3808 m); and Gothic Mt., 12,600 ft (3840 m). Each of these peaks had a modest colony of *E. anicia*. Larval foodplants, *Besseya alpina* Rydberg (White, 1979), did not occur below 11,500 ft (3500 m), so each peak was separated from each other peak by habitat unfavorable to *E. anicia*. *Besseya alpina* is strictly an alpine plant (Harrington, 1954).

From 5 to 31 July 1978, a mark-release-recapture program was conducted. Each butterfly was given its own number in a magic marker code (Ehrlich & Davidson, 1960), with different colors used for marking on the separate peaks. Each peak was climbed in turn and as many butterflies as possible marked on each. The condition, sex, and capture site of each butterfly was recorded with its number. These data (Appendix) allowed the mapping of intra-peak movements, while the colors used in the marks signified the peak on which the butterfly had first been marked.

The time of ascent from base camp to *Euphydryas* habitat was about 2 h; descents took about 1 h. Four days were missed due to inclement weather and early descents from the peaks were forced four times by thunderstorms. Poor weather reduced flight on three additional days.

Population sizes were estimated from mark-release-recapture data by the Lincoln Index method using males only and then multiplying by two (Ehrlich et al., 1975). This provided estimates for all days except the first day that butterflies were marked on a given peak. It was assumed that the population changed at a constant (geometric) rate between marking days. Estimates of the numbers of individuals that flew at a given site over the course of the flight season were made by summing the numbers estimated for each calendar day and dividing by the estimated average residence time. The first and last days of the flight season were estimated from the number of butterflies handled on the first and last marking days. The average residence time was calculated as the reciprocal of one minus the probability of presence from one day to the next.

The probability of daily presence was assumed to be constant over the season and was estimated from recapture data as follows: on the third and each subsequent marking day it is possible to compare the rates of recapture of different classes of marks, that is, those marked

on different days. The geometric mean of the resulting ratios was calculated, weighting each sample (comparison of one class to another) by approximately the harmonic mean of the numbers of butterflies recovered from each class.

RESULTS AND DISCUSSION

The sizes of these *Euphydryas* populations, while at least an order of magnitude smaller than that at Cumberland Pass (Cullenward et al., 1979), were larger than expected, based on the modest sizes of these alpine zones. The estimates given below are rough, based on mark-release-recapture data. In spite of relatively small areas of available habitat, population sizes were greater than a few hundred individuals per peak. During the season there were probably 3000–5000 butterflies on Gothic Mountain, 1600–3200 on Bellview, 500–1000 on Baldy, and 400–600 on Cinnamon. The total present on all four peaks on any one day might have been 2000–4000.

The flight seasons differed from one peak to another and were atypically long for *Euphydryas* (White, unpubl.; M. C. Singer, pers. comm.). The season on Bellview preceded the season on Gothic by a week to ten days. The lengths of the flight seasons were estimated as six weeks or more, based on numbers flying at the start and finish of the study. This concurs with previous estimates for *E. anicia* (Cullenward et al., 1979).

Residence times, estimated by the method described, were greater than residence time estimated by the method of Ehrlich (1961), as expected. Butterflies seemed to live about as long as most *Euphydryas* under field conditions (Gothic males—10.4 days, Bellview males—8.9 days). Ten butterflies were recaptured more than two weeks after marking.

Recaptures of 189 marked individuals (229 recapture events) indicated the following. First, there were differences between the sexes. Second, patterns of movement varied between topographic areas within single peaks. Third, the patterns varied among peaks. Fourth, some inter-peak dispersal occurred.

Dividing Bellview and Gothic into areas of high and low butterfly density, one observes the same kind of difference that Cullenward et al. (1979) found for *E. anicia* at Cumberland Pass (CL) in 1976. More densely populated areas possess larger proportions of females, more nectar, and more foodplants. They tended to be north-facing slopes (BV, CL) protected from weather (of other directional origins than north) by higher ridges and shoulders. Less densely populated areas tended to be ridges and peaks, sometimes above the more densely populated areas. Butterflies marked in the more favorable areas were
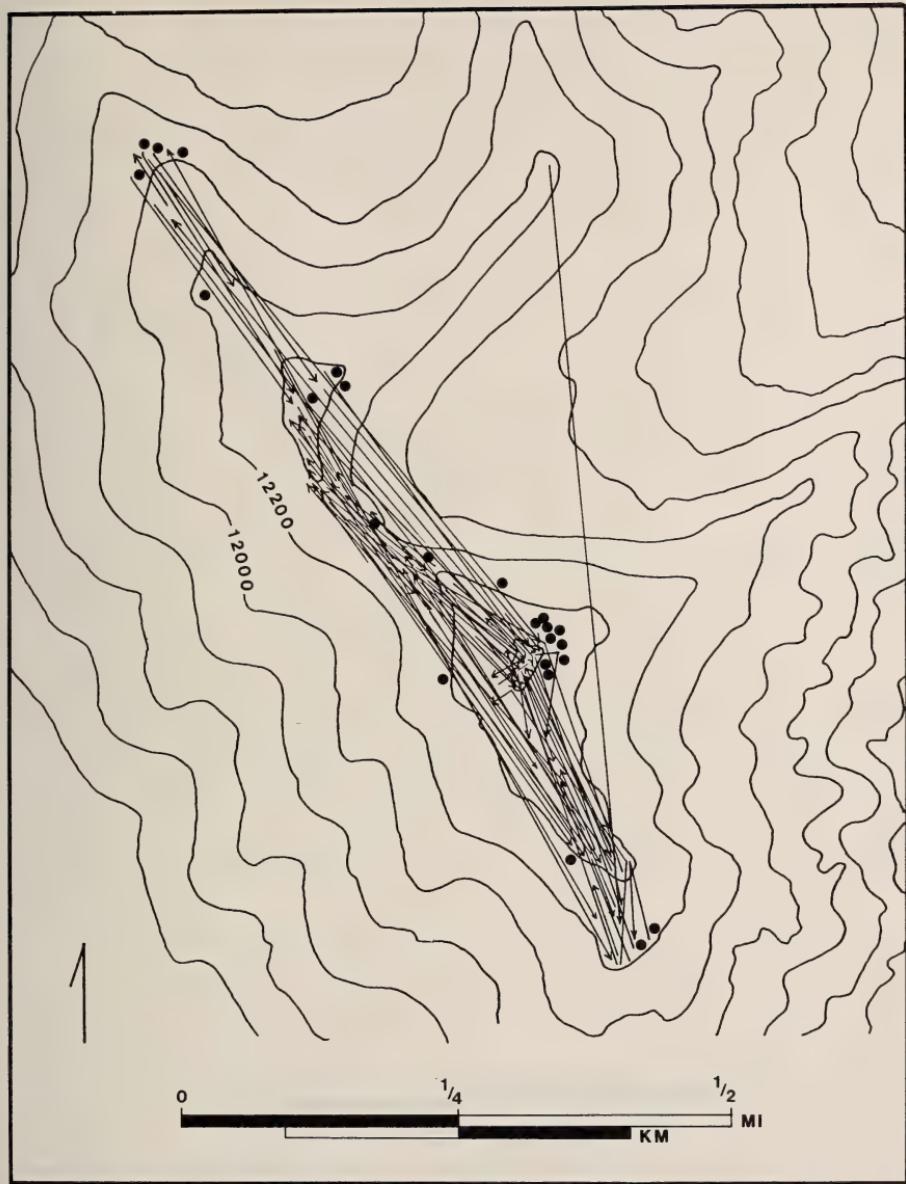
FIG. 2. Contour map of Gothic Mountain showing movements of *E. anicia* males. Each dot represents two recaptures in area of original capture.

more likely to be recaptured than those marked in the less favorable areas (Bellview males, 34/121 vs. 26/185, df = 1, G = 9.02, P < .005; Sokal & Rohlf, 1969).

Female *E. anicia* were recaptured in numbers only on Bellview in
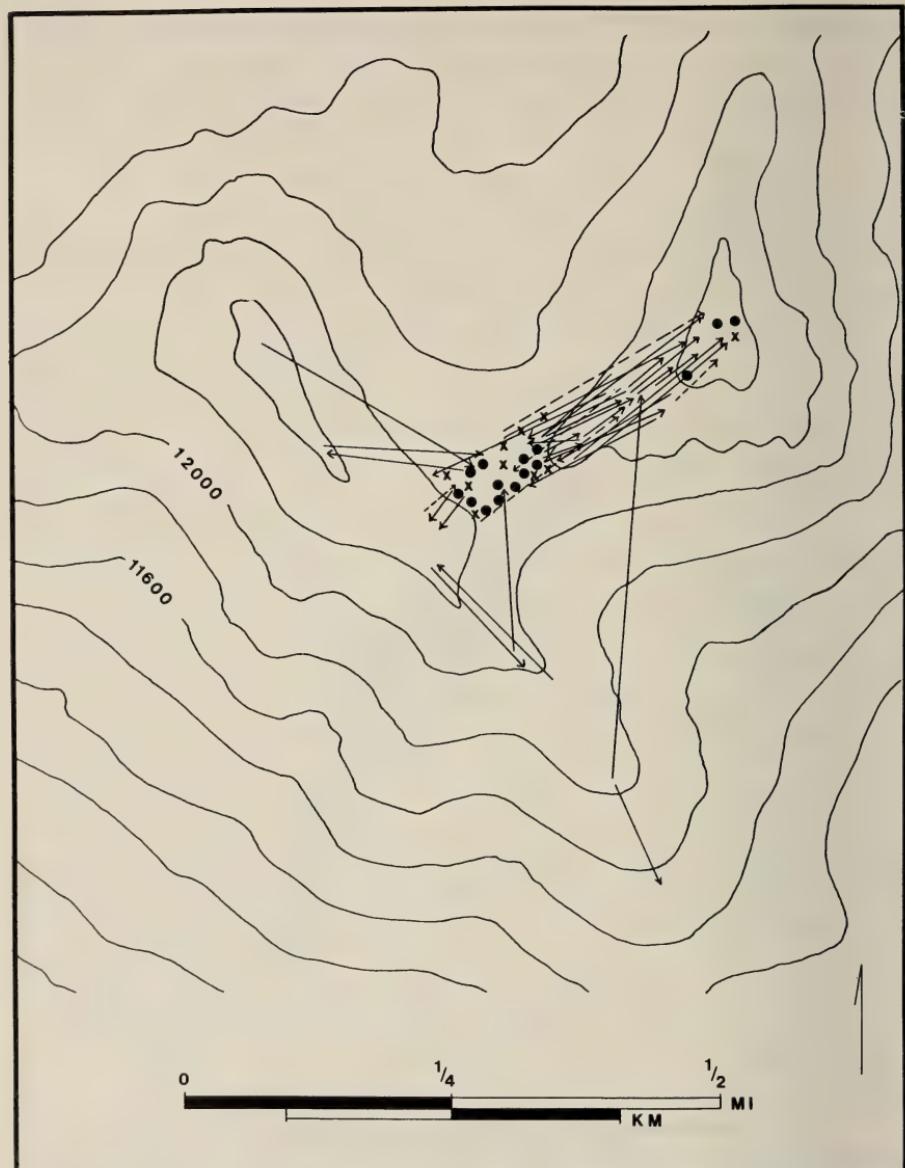
FIG. 3.   Contour map of Bellview showing movements of *E. anicia*. Dots represent males and x's represent females recaptured at or near point of previous capture. Solid arrows represent male movements, dashed arrows represent female movements.

this study (Fig. 3). Average movement between recaptures was 18 ± 59 m ($\bar{x} \pm s$; n = 25), similar to that observed at Cumberland (18 ± 44 m, n = 32). Males on Bellview averaged 65 m between recaptures (n = 63, s = 109 m), comparable to the 75 m observed at Cumberland

(n = 173, s = 129 m). This sexual difference has been found for all alpine *Euphydryas* populations studied (White, 1973).

Dispersal differences among peaks paralleled those found within peaks. Dispersal within Gothic appears to be more extensive than at Bellview. Gothic males moved 146 ± 222 m between recaptures (n = 109, s = 222 m), more than twice as far as those on Bellview (Fig. 2). Velocity per day (v_i of Scott, 1975) averaged 23 m for Gothic males and 8 m for Bellview males. In addition, the kurtoses (departures from a normal curve) of the data from the two sites differed (GM, n = 107, g_2 = 5.61, s.e. = 0.47; BV, n = 62, g_2 = 7.11, s.e. = .60; t = 1.94, df = 167, .05 < P < .06; Sokal & Rohlf, 1969; J. Matta, pers. comm.). The pattern of movement on Gothic was not as leptokurtotic as that on Bellview. Gothic Mountain, while divisible into more favorable and less favorable areas, had no area with the very high density of butterflies observed in the favorable areas of Bellview and Cumberland. Favorability of *Euphydryas anicia* habitat is defined as having both nectar and larval foodplants in densities such that a flight of a few meters would pass by examples of each. Mt. Baldy was less favorable than Gothic, and less densely populated.

Transfers from one peak to another were observed only from Baldy to Cinnamon (see below). Long distance dispersal, then, seems to arise from less densely populated, less favorable areas. It is unclear whether the different kinds of areas selectively favor different, genetically determined (intrinsic) dispersal behavior or whether the butterflies native to any area would respond similarly. If the latter case is correct, a corollary question is whether the butterflies respond to male density, female density, nectar availability, or to a combination of factors.

Whatever the cause of the observed movements within the peaks, it seems likely that the result is spatially extensive demes possessing large numbers of individuals. Dispersal increases the effective area of a deme and thus keeps the numbers of individuals within demes high, even as densities decrease. Such behavior would decrease the effects of genetic drift among areas within peaks, and increase the rate of colonization of new or empty habitats within peaks. Observed dispersal makes it clear that separate population units do not exist within peaks of the size studied. Each peak contains an essentially panmictic unit.

One displacement experiment was attempted. Fifty-seven males and 28 females were moved from Bellview down to a point on the road approximately equidistant from Bellview, Baldy, and Gothic. One female was recovered in her area of origin on Bellview 3 days after release. One male was recovered 300 m downslope from origin

on Bellview 13 days after release and one male was recovered on Gothic Mountain 2 days after release. The low recovery rate may be due to the tired condition of the displaced animals and to inadequate subsequent coverage of these peaks. The recovered animals moved 3 km from an elevation of 2955 m to at least 3534 m. Such movements indicate the potential for dispersal that these butterflies possess.

Two *bona fide* transfers between peaks were observed. One male moved 2 km from the west end of Baldy to Cinnamon Mt.; another male moved 2.2 km from the east end of Baldy to Cinnamon Mt. Three percent of the butterflies marked on this sparsely populated area of Baldy are thus known to have transferred out. These transfers are notable in five respects. The elevation between the peaks dropped 300–450 m. The flora changed from alpine to alpine-meadow; there were no oviposition plants in the intervening areas. The transfers were against the prevailing winds. The peak of origin seemed relatively unfavorable as an *Euphydryas* habitat. This may indicate purposeful movement from one peak (demographic unit) to another at a rate between 0.1% and 10%, assuming the real rate is within an order of magnitude of that observed (2/229 recapture events). Assuming post-transfer reproductive success, such a rate would almost eliminate genetic drift as a force differentiating the demographic units. One would not expect significant differences in the frequencies of selectively neutral alleles among populations experiencing such transfer rates. So far no significant genetic differences have been found among these populations (C. E. Holdren, P. R. Ehrlich, unpubl.), so that in some respects all four peak colonies appear to be part of the same large deme.

CONCLUSIONS

The following conclusions are drawn from these data:

1. Transfer among separate peaks probably occurs at rates between .001 and 0.10, great enough to limit divergence of neutral allele frequencies by genetic drift, assuming that transfers are reproductively successful.

2. Demes of this species are large in area and fairly large in numbers of individuals; they may include several separate peaks.

3. Dispersal rates increase as the apparent favorability of the point of origin decreases.

4. Flight seasons are long and vary in timing from one peak to another.

5. Female *E. anicia* are more sedentary than males.

ACKNOWLEDGMENTS

LITERATURE CITED

BROWN, F. M., J. D. EFF & B. ROTGER. 1957. Colorado Butterflies. Denver Mus. Nat. Hist., Denver. 368 pp.

BRUSSARD, P. F. & P. R. EHRLICH. 1970. Contrasting population biology of two species of butterfly. Nature 227: 91–92.

CULLENWARD, M. J., P. R. EHRLICH, R. R. WHITE & C. E. HOLDREN. 1979. The ecology and population genetics of an alpine checkerspot butterfly, *Euphydryas anicia.* Oecologia (Berl.) 38: 1–12.

EHRLICH, P. R. & S. E. DAVIDSON. 1960. Techniques for capture-recapture study of Lepidoptera populations. J. Lepid. Soc. 14: 227–229.

EHRLICH, P. R. & L. E. GILBERT. 1973. Populations structure and dynamics of the tropical butterfly *Heliconius ethilla.* Biotropica 5: 69–82.

EHRLICH, P. R. & P. H. RAVEN. 1969. The differentiation of populations. Science 165: 1228–1232.

EHRLICH, P. R. & R. R. WHITE. 1980. Colorado checkerspot butterflies, isolation, neutrality, and the biospecies. Am. Nat. 115: 328–341.

EHRLICH, P. R., R. R. WHITE, M. C. SINGER, S. W. MCKECHNIE & L. E. GILBERT. 1975. Checkerspot butterflies: a historical perspective. Science 188: 221–228.

GILBERT, L. E. & M. C. SINGER. 1973. Patterns of dispersal and gene flow in a butterfly species. Am. Nat. 107: 58–72.

HARRINGTON, H. D. 1954. Manual of the Plants of Colorado. The Swallow Pr., Chicago. 666 pp.

HOWE, W. H. 1975. The Butterflies of North America. Doubleday, Garden City. 633 pp.

LEWONTIN, R. C. 1974. The Genetic Basis of Evolutionary Change. Columbia Univ. Pr., New York. 346 pp.

MCKECHNIE, S. W., P. R. EHRLICH & R. R. WHITE. 1975. Population genetics of *Euphydryas* butterflies. I. Genetic variation and the neutrality hypothesis. Genetics 81: 571–594.

SCHRIER, R. D., M. J. CULLENWARD, P. R. EHRLICH & R. R. WHITE. 1976. The structure and genetics of a montane population of the checkerspot butterfly, *Chlosyne palla.* Oecologia (Berl.) 25: 279–289.

SCOTT, J. A. 1975. Flight patterns among eleven species of diurnal Lepidoptera. Ecology 56: 1367–1377.

SOKAL, R. R. & F. J. ROHLF. 1969. Biometry. Freeman, San Francisco. 641 pp.

WATANABE, M. 1978. Adult movements and resident ratios of the black-veined white, *Aporia crataegi,* in a hilly region. Jap. J. Ecol. 28: 101–109.

WATT, W. B., F. S. CHEW, L. R. G. SNYDER, A. G. WATT & D. E. ROTHSCHILD. 1977. Population structure of pierid butterflies. I. Numbers and movements of some montane *Colias* species. Oecologia (Berl.) 27: 1–22.

WHITE, R. R. 1973. Community relationships of the checkerspot butterfly, *Euphydryas editha.* Ph.D. diss., Stanford University, Stanford, Calif. 90 pp.

——— 1979. Foodplant of alpine *Euphydryas anicia* (Nymphalidae). J. Lepid. Soc. 33: 170–173.

APPENDIX
Mark-release-recapture data

	GM (males)	BV (males)	BV (females)	GM (males)[3]	CM (males)[4]
Number marked[1]	412	288	115	76	69
Number sampled	78	114	40	1	0
Number retaken[2]	85	51	25	20	8
Recapture events[2]	109	63	25	24	6
Average distance moved between recapture events (d)[5]	146 m	65 m	18 m	—	—
s	222 m	109 m	59 m	—	—
Net range of individuals (R)	169 m	67 m	18 m	—	—
s	232 m	111 m	59 m	—	—
Average time between recapture events (t_i)	5.7 days	6.7 days	6.2 days	—	—
Average time from first to last capture (T)	7.0 days	7.3 days	6.2 days	—	—
Average velocity per day (v)	22.6 m/day	8.0	3.0	—	—

[1] Omits last day at each site.
[2] Omits displaced butterflies (3 recaptured individuals, 3 events).
[3] Twelve females marked, 1 sampled, no recaptures.
[4] Nine females marked, none recaptured.
[5] d_i, R, t_i, T, and v refer to statistics of Scott (1975).

GENERAL NOTES

ABERRANT SPECIMEN OF *CHLOSYNE LACINIA* FROM CENTRAL TEXAS RESEMBLES TROPICAL FORM

Throughout its geographical range from the southern United States to Argentina, *Chlosyne lacinia* (Geyer) exhibits wing pattern variation which is "hard to match in any other butterfly" (p. 405, Higgins, 1960, Trans. R. Entomol. Soc. Lond. 112: 381–475). The phenotype in central and southern Texas is *adjutrix* Scudder which is best considered a form of *saundersi* Doubleday, a phenotype which occurs throughout the range of this species (Godman & Salvin, 1882, Rhopalocera. Biologia-Centrali-Americana. Vol. 36–38; Higgins, op. cit.). Phenotypes of this species exhibit a near continuum of variation from the highly fulvous nominate *lacinia* Geyer to the melanic *quehtala* Reakirt (Godman & Salvin, op. cit., Pl. 19, Fig. 3–17).

Butterflies from Texas exhibit substantial variation within the *adjutrix* form; such variation has previously received taxonomic attention. An early collecting trip to south Texas ("Gulf region near Corpus Christi") yielded specimens referable to *adjutrix*, *saundersi* and *mediatrix* Felder and Felder (Aaron & Aaron 1884, Papilio 4: 172–182). This latter name was considered by Higgins (op. cit.) to be synonymous with nominate *lacinia*. Although variation is considerable among Texas specimens, the necessity for all of these names appears doubtful. In order not to create confusion *lacinia* populations from central and south Texas will be referred to *adjutrix*.

Normal wing pattern and pigmentation for *adjutrix* are as follows:

Dorsal. Brownish-black ground color; broad median band, orange-brown in color, fading intensity and broadness as it approaches costal margin of FW; margins black; normally three post-basal and submedian spots, variable in size and shape, orange in color; postmedian spots white, normally seven. May be adjacent to or separated by ground color from median band; submarginal spots light yellowish-brown, two or three may be distinct, others obscured by ground color; marginal spots white; margin of HW orange.

Ventral. Brownish-black ground color; broad median band completely yellow on HW, whitish in costal area of FW, remainder of FW band yellowish and red orange; post-basal and submedian spots yellowish, variable in size, shape and number (especially HW); post-median spots white; submarginal spots yellowish; marginal spots white, red-orange anal spot.

A highly aberrant form of *adjutrix* is in my collection. This aberration was collected on 10 October 1971 along Barton Creek in Zilker Park, Austin, Travis Co., Texas, by L. E. Gilbert. At the time of collection this anomalous male insect was courting a typically patterned female *adjutrix*. The aberrant form may be described as follows (due to the lack of congruity between forewing and hindwing surfaces on both dorsal and ventral surface as in typical *adjustrix*, the four wing surfaces are discussed separately):

DFW. Post-basal and submedian spots absent; median band absent except for the four most-costal spots, two most-costal spots white, other two creamish; postmedian spots and marginal spots normal; submarginal spots whitish.

DHW. Post-basal and submedian spots absent; median band absent except for four barely-visible (pin-prick) spots, orange in color; postmedian, submarginal and marginal spots normal; anal margin brownish black except for anal spot (red-orange) which corresponds with VHW anal spot.

VFW. Post-basal and submedian spots absent; median band reduced except for four costal spots, coloration same as DFW; postmedian and marginal spots normal; submarginal spots whitish.

VHW. Post-basal, submedian and median spots absent; postmedian, submarginal, marginal spots and anal spot normal; slightly asymmetric in that anal margin of left

VHW has thin yellowish band which does not extend as far as anal spot while right VHW anal margin is brownish black.

Both dorsal and ventral surfaces of this aberration are similar to an insect portrayed by Godman & Salvin (op. cit., Pl. 19, Fig. 12–13) which Higgins (op. cit.) refers to *paupera* (C. & R. Felder). The example illustrated by Godman & Salvin has an orange-red spot on both dorsal and ventral forewing which my example lacks. However, Higgins (op. cit.) states that there is "much variation" among specimens which he assigned to this taxon. Godman & Salvin (op. cit.) considered this form to be a link between nominate *lacinia* and *adelina* Staudinger which is an extreme melanic form (considered a form of *quehtala* Reakirt by Higgins, op. cit.). Higgins (op. cit.) studied eighteen specimens of this form from six localities scattered from Costa Rica to Peru. The form *paupera* has not been reported from Mexico (Hoffman, 1940, An. Inst. Biol. Mex. 11: 639–739).

In comparing this aberration from central Texas to a form from tropical America, I am not implying that this particular individual is a long-distant migrant from these southern areas. On the contrary I believe that this form represents expression of alleles which are normally suppressed in central Texas populations. A supergene complex probably controls expression of wing phenotypes.

The specimen was collected during a period of extreme abundance of *adjutrix* in central Texas. Heavy late summer rains triggered a population explosion of *adjutrix* which had been very rare for the previous 12 months because of an extreme drought. This aberrant specimen is a further example of increased phenotypic variability during high population levels due to relaxed selective pressures (see e.g., Tetley, 1947, Ent. 80: 177–179; Ford, 1964, Ecological Genetics, Methuen).

Lack of data concerning progeny of the central Texas aberrant does not permit an absolute statement concerning the genetic and/or environmental triggers involved in the production of this phenotype. However, the internal integrity of the design suggests a genetic origin. No spots are "blurred" into bands as is often the situation in environmental aberrations, including those which may be experimentally produced by manipulation of environmental parameters, particularly lowered temperature (Dimock, 1968, J. Lepid. Soc. 22: 146; Shapiro, 1974, J. Res. Lepid. 13: 57–62).

A substantial classification system for aberrations was developed during an earlier study period of butterfly taxonomy (see discussion by Gunder, 1927, Ent. News 37: 263–271). The aberrant form of *Chlosyne lacinia* var. *adjutrix* described above is best classified as a transitional form which describes "individuals which occur irregularly within a species or within a race and which by change of color or by change of pattern graduate with persistent characteristic similarity from near parental type up to definitely limited variation away from parental type" (Gunder, op. cit.: Pl. X). Note the statement by Higgins (op. cit.) that *paupera* is a rather variable form. This form may best be considered as a phenotypic expression of allele combinations normally suppressed by a supergene complex. Under certain environmental conditions population levels of *adjutrix* expand rapidly to very high levels. During this time of temporarily relaxed selection, individuals with synapsis occurring within the supergene are able to survive.

These transitional forms are normally of no taxonomic or evolutionary significance. Such individuals may reproduce but the action of normal selective forces will soon cause their replacement by normal phenotypes. In rare cases, however, a population of the aberrant pattern might establish a local "race" and could, theoretically, produce a taxon of phylogenetic significance.

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THE STATUS OF *PAPILIO MACHAON RATHJENSI* AND
ITS RELATIONSHIP TO OTHER ARABIAN POPULATIONS
(PAPILIONIDAE)

In 1931 Dr. C. Rathjens captured a series of 4 male and 3 female specimens of *Papilio machaon* Linné 1758 near Sana'a in the high mountains of the present Yemen Arab Republic. This locality was some 1200 km from the closest known locality of *machaon* at Hofuf in eastern Saudi Arabia. It was described as ssp. *rathjensi* by Warnecke in 1932 (Int. Ent. Z., 25: 473–476). The chief characteristic of this subspecies is the broad black band of the hindwing upperside which reaches the cell and even encroaches upon it; together with the strongly blackened base of the hindwings this lends *rathjensi* a very distinctive appearance. It is certainly one of the best defined subspecies of *machaon*. The type series, which remained unique, appears to have been destroyed in the giant bombing raids on Hamburg during the second world war.

Eller (1936, Abh. Bayer. Akadem. Wiss., Math.-Nath., NF36; 1939, Verh. VII Int. Kongr. Ent., Berlin, 1: 74–101) on morphological grounds believed that *rathjensi* was allied to ssp. *saharae* Oberthür, a subdesert form distributed along the fringes of the Sahara from Morocco to the Sinai. Eller was not permitted to dissect a specimen to check whether the harpe in the male genitalia of *rathjensi* matched the characteristic reduced harpe of *saharae*. Seyer, in a recent revision of *machaon* (1974, Mitt. Ent. Ges. Basel, 24: 64–117 and 26: 65–87, 97–145), was able to take the matter no further, hardly mentioning the Arabian taxa.

Thanks to the kindness of Mr. P. Carden I obtained two specimens of *P. machaon rathjensi* collected near Taizz, elev. 1100 m, in 1974 when he was ambassador of Great Britain to the Yemen Arab Republic. In all respects they match the original description and its accompanying photographs. On dissection the harpe of the male genitalia was found to match that of ssp. *saharae* (see Fig. 1). In addition to the differences in morphology and genitalia, the larva of ssp. *saharae* differs from other subspecies of *machaon* (Clarke & Sheppard 1956, Evolution 10: 66–73), but unfortunately nothing is known about the biology of *rathjensi*. It is well known that the male genitalia of butterflies is subject to both individual and geographic variation. Turner (1963, Trans.
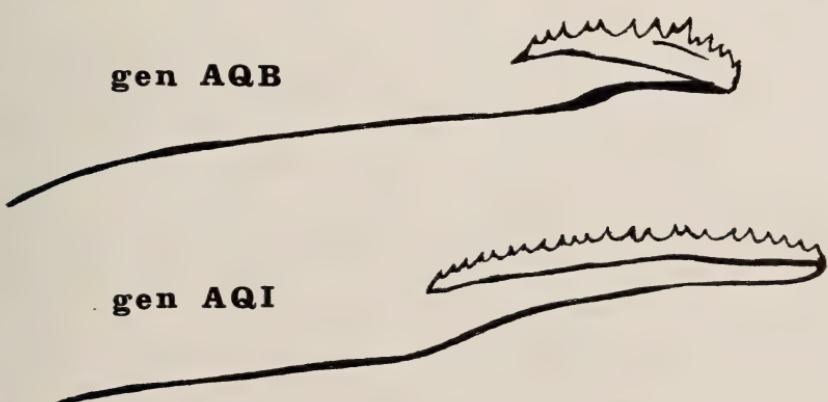
FIG. 1.   The harpe of the male valve in *Papilio machaon*. Gen AQB illustrates spp. *rathjensi* from Yemen; gen AQI ssp. *syriacus* from the Hofuf area (codes refer to the author's slide collection).

FIG. 2.　*Papilio machaon* from Arabia. Top row, ssp. *rathjensi* from Yemen; bottom left, ssp. *syriacus* from the oasis at Hofuf in eastern Saudi Arabia; bottom right, ssp. *muetingi* from Oman (slightly smaller than natural size).

R. Ent. Soc. Lond. 115: 239–259) illustrates this well in the African *Papilio dardanus* Brown. However, given the fact that literally thousands of *P. machaon* from all over its range have been dissected, none of which show the degree of reduction in harpe found in *saharae,* one feels safe in assuming a close relationship between *rathjensi* and *saharae.*

That this should be so is most interesting since the other Arabian populations of *machaon* are not related to *saharae.* That of the Hofuf oasis (ssp. *arabensis* Eller (*nomen nudum*)) is probably best referred to ssp. *syriacus* Verity, though there are small differences in detail (form of tail, form of median band on the forewings). That of northeastern Oman is clearly ssp. *muetingi* Seyer (=*iranus* Eller (*nomen nudum*)). Both of these populations have the normal long harpe structure; a specimen from Hofuf is shown in Fig. 1.

These findings invalidate the otherwise attractive suggestion made by Wiltshire (1945, Proc. R. Ent. Soc. Lond. 20: 6–25) that *machaon* invaded the high mountains of Yemen along the Red Sea coast and subsequently moved northeast to Hofuf. They certainly invaded independently. *P. machaon syriacus* still exists in the Jordanian deserts. Probably scattered populations of *machaon* survived in Central Arabia until recently, but the gradual desiccation processes of the past 5000 years forced it to adapt to oasis conditions, hence its current isolation in the huge oasis complex around Hofuf. Although Oman has more rain and more dependable rainfall than eastern Saudi Arabia, the Omani population has also largely adapted to oasis conditions. Despite the distance, *P. machaon syriacus* could be a recent immigrant rather than a relict. However, circumstantial evidence supports the relict theory. First, there are relict populations of other Palaearctic species in the area which are decidedly non-migratory, the most
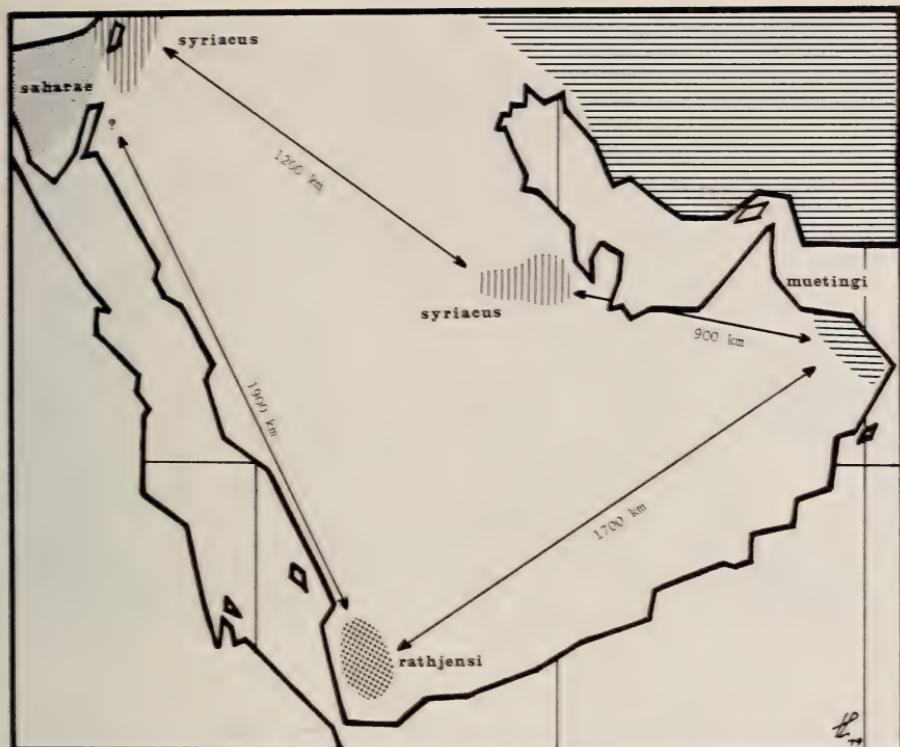
FIG. 3. Distribution of *Papilio machaon* in Arabia. Populations of *machaon* most closely related to ssp. *syriacus* extend to Bagdad in Iraq just north of the map.

important in the Rhopalocera being *Melitaea persea sargon* Hemming. Second, ssp. *iranus* would have been much more likely to colonize than *syriacus* (Fig. 3).

Zoogeographically we are faced with an interesting situation. Arabia, which is currently populated by a mixture of Palaearctic migrant species, eremic species and tropical species, contains three well established and totally isolated populations pertaining to three different subspecies of the typically Palaearctic, non-migratory *Papilio machaon*. Ssp. *rathjensi* probably invaded Yemen during an interglacial period; ssp. *syriacus* probably was widely distributed in central parts of Arabia during the postglacial pluvial optimum and is thus a recent isolate. It is in the process of subspeciation and has been forced to adapt to an oasis environment. The Omani populations of ssp. *muetingi* are isolated from the Iranian by water but it is doubtful whether the distances are sufficient to ensure that gene flow between Omani and Iranian populations has been totally cut off.

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FIELD OBSERVATIONS OF LARVAL BEHAVIOR OF *DATANA INTEGERRIMA*
(NOTODONTIDAE) IN ILLINOIS

Black walnut, *Juglans nigra* L., is an important nut, ornamental, and timber species in the eastern United States. Tree farmers, homeowners, nut growers, and foresters plant many acres of this tree each year. The role of insects in tree development is of concern to the owners. The walnut caterpillar, *Datana integerrima* G. & R., is a major defoliator of black walnut and other species of the Juglandaceae. This study was initiated in 1975 to better understand the relationship of the walnut caterpillar and other insects to the establishment and development of trees in such plantings.

Datana integerrima was described by Grote & Robinson in 1866 (Proc. Entomol. Soc. Philadelphia 6: 12–13). Their larval description was limited to the fifth stage. Packard (1895, Mem. Nat. Acad. Sci. USA 7: 105, 120–122) described and illustrated the five larval stages. Life history studies were made by Baerg (1928, Ark. Agric. Exp. Sta. Bull. 224: 9–16), Haseman (1940, Mo. Agric. Exp. Sta. Bull. 418, 15 p.), and Hixson (1941, Okl. Agric. Exp. Sta. Bull. B-246, 29 p.). Limited bionomic and behavioral data are available in these studies. The insect is reported to feed on apple (Grote & Robinson, op. cit.), willow, honey locust, thorn, beech, apple, and oak (Packard, op. cit.; Forbes, 1911, Ill. Agric. Exp. Sta. Bull. 151: 470–472; Houser, 1918, Ohio Agric. Exp. Sta. Bull. 332: 226–229), and azalea (Cochran, 1976, U.S. Dept. Agric. Coop. Plant Pest Rep. 1(40): 675).

Information presented here is based on field observations of colonies of walnut caterpillar larvae in central and southern Illinois. Egg masses and larval colonies found on the foliage of large black walnut, pecan (*Carya illioensis* (Wangenh.) K. Koch), the hickories (*Carya* spp.), and English walnut (*Juglans regia* L.), were clipped off with pruners and transferred onto twigs or leaflets of smaller trees of the same species. The twigs and leaflets were tied or clipped to the foliage of the smaller trees to prevent dislodgment. Placement of the egg masses and colonies on smaller trees facilitated close observation of larval behavior, collecting predators and parasites, and recovery of mature larvae. Other than the initial transfer, the study was conducted under natural conditions. Movements and behavioral reactions of some colonies that defoliated the trees were recorded. Approximately 75 colonies were used (ca. 46,500 larvae), but behavioral characteristics were not quantified. Most observations were made during daylight hours. However, some colonies and egg masses were collected at night and placed in plastic bags to be relocated the next day.

Egg masses are always found on the lower leaflet surface. The larvae are gregarious and, upon eclosion, first stage larvae spin silk over the egg mass then move to the upper leaflet surface while depositing a silken trail during their movements. As other larvae emerge they crawl over and follow the trails spun by earlier emerging larvae, while spinning their own silken trails. The larvae devour the surface tissues, giving the leaflet a skeletonized appearance (Fig. 1). After feeding on the upper surface the larvae expand their feeding activities to nearby leaflets, and then feed on either surface.

Second stage larvae feed from the edge of the leaflet and devour the entire leaflet except the larger veins, later they leave only the main vein. Third stage larvae initially leave the main vein, but later devour it leaving only a petiolar stub as do the fourth and fifth stages.

Most movements of the larvae on the leaflets, rachides, branches, and stems occur as a colony. During these movements the larvae spin large quantities of silk on the branches, twigs and leaf rachides. After initially feeding, individual larva wander short distances over the leaf rachis and adjacent foliage depositing silk as they wander, but wandering larvae usually return to the main colony after a brief period of time, maintaining the contiguity of the colony. A rachis, twig, or small branch may be completely covered by silken trails as a result of this wandering. Larvae may use silk deposited

FIGS. 1–4. **1,** black walnut foliage skeletonized by first stage walnut caterpillar larvae; **2,** a colony of fourth stage walnut caterpillar larvae molting to the fifth stage on the foliage of a black walnut tree; **3,** a fifth stage walnut caterpillar larva returning to the foliage along a silken trail; **4,** colonies of fourth and fifth stage walnut caterpillar larvae on the same foliage of a black walnut tree.

during their wanderings as a means by which to return to the colony and the colony may later follow the silken trails when moving to molting or new feeding sites on the host plant. Movement away from the main colony appears to be an age dependent factor. The larvae become less gregarious during the 5th stage and tend to separate into smaller groups.

Just prior to molting the larvae congregate and spin a molting pad to which they cling during the molting process. The first and second molts generally occur on the foliage. The third and fourth molts normally occur on the bole of the tree or larger branches, occasionally these molts take place on the foliage (Fig. 2). In a large fourth stage colony the molting pad is usually large (ca. 24 × 24 cm) and the larvae are found on and in the pad. Upon completion of the molting process the larvae return to the foliage following silken trails deposited earlier (Fig. 3). They generally return to the same foliage area they were in before molting. If the foliage is depleted the larvae seek additional food on the same branch before moving to other branches. As the larvae mature they tend to move to higher branches.

Larvae of different stages congregate together if there is more than one colony on the same tree (Fig. 4). Different stages may occasionally be found at the same molting site and all stages frequently feed on the same leaflets during periods of high population. The larvae mingle on all sized trees during these periods, particularly when the silken trails of the colonies cross. The larvae are defensive. When threatened, the larvae arch their bodies so as to raise the thorax and posterior body segments from the surface of the substrate. If the disturbance persists, the larvae often secrete a droplet of fluid (found to have an approximate pH of 9.5) from between the mandibles and make quick

TABLE 1. Plants on which walnut caterpillar larvae were found after they abandoned defoliated black walnut and other host trees in Illinois.

Plant species	Common name
Acer saccharum Marsh.	sugar maple
Erigeron annuus (L.)	daisy fleabane
Erigeron canadensis (L.)	horseweed
Festuca sp.	tall fescue
Liquidambar styraciflua L.	sweetgum
Liriodendron tulipifera L.	tuliptree
Pinus sylvestris L.	Scotch pine
Platanus occidentalis L.	sycamore
Quercus imbricaria Michx.	shingle oak
Rosa multiflora Thunb.	multiflora rose
Rubus sp.	blackberry
Solidago sp.	goldenrod
Ulmus alata Michx.	winged elm

up-and-down or sideways movements with the anterior and posterior segments of the body striking the surface of the leaflet. Under natural conditions the entire colony usually reacts in unison. This response is frequently sufficient enough to distract many predators and parasites.

A larva need not be touched or prodded to initiate the alarm or defensive reaction. Touching the leaf rachis, leaflet, or the branch on which the larvae are clinging often induces the defensive reaction in a colony. Little or no reaction to wind is seen.

Three to four days after the last molt, larvae continue to feed, but readily drop from their feeding site to the ground when the foliage and/or branches they occupy are shaken. The larvae do not spin silk as they drop. This reaction, displayed only by nearly mature fifth stage larvae when they are disturbed, is probably defensive. At this stage the larvae are turgid and some are injured upon hitting the ground or other objects. Vibrations, such as those caused when a branch is touched or even those caused by an ichneumonid alighting on a leaflet are probably the causative factor in initiating the larval defensive response.

Walnut caterpillar larvae abandon trees when the foliage becomes sparse or when the tree is defoliated. The larvae scatter in all directions upon leaving the tree and are apt to ascend any nearby plant. Third, fourth, and fifth stage larvae, abandoning defoliated trees, disperse around the base of the tree; some return and reascend the tree. After crawling over several branches, larvae reascending the tree soon descend and disperse. Initially the larvae move only short distances from the base of the tree, then they move to greater and greater distances. When a larva travels a distance of ca. 2 m it generally continues in a direction away from the tree it abandons. This dispersal process continues for several hours. They ascend grass stems, weeds, other nearby trees (Table 1) and crawl through the litter on the ground. The larvae do not feed on these plants and abandon them in ca. 24 hours. Directional polarized light from the sun appears to have little influence on larval orientation since many larvae wander north, as well as other directions, upon abandoning defoliated host trees (Doane & Leonard, 1975, Canad. Ent. 107: 1333–1338).

Farris & Appleby (1979, Univ. Ill. Agric. Exp. Sta. DSAC 7: 12–18) indicate larvae feed and survive only on species of Juglandaceae. Early reports of larval feeding on other plants may be due to larval abandonment of host trees and patterns associated with search for suitable food resources. Species of *Datana* larvae are difficult to distinguish in the first four stages. Early workers may have misidentified the different *Datana* species, resulting in the present confusion concerning their host plants.

At maturity the larvae become very flaccid, are restless, cease feeding, release their grasp and roll off the branch or rachis of the host tree and drop to the soil. Upon reaching the ground the larvae remain quiet for 3–4 s then begin to wander, finally burrowing into the litter and soil where pupation occurs. Their flaccid condition suggests that the digestive tract is purged before dropping and this probably offers some protection against injury upon landing.

The larvae generally pupate 1–3 cm deep in sod, 1–7 cm in loose soil and in heavy litter on the ground. They do not spin a cocoon before pupating. A cell is made in the soil or litter around the pupa by larval/pupal movements made during the pupation process.

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ANTS ASSOCIATED WITH *HARKENCLENUS TITUS, GLAUCOPSYCHE LYGDAMAS*, AND *CELASTRINA ARGIOLUS* (LYCAENIDAE)

Larvae of many lycaenid species are assoicated with ants. The latter feed on secretion from the larvae and presumably offer them protection against predators and parasitoids. Despite the fact that a number of North American lycaenid larvae are reported to be myrmecophilous, with few exceptions, the associated ants are largely unknown. During 1976 and 1977, we made observations of *Harkenclenus titus* (Fabricius), *Glaucopsyche lygdamas* (Doubleday), and *Celastrina argiolus* (Linnaeus) at several localities in Washtenaw Co., Michigan. Although all of these species have long been known to be myrmecophilous, there are few published records of the species of ants involved (see below). These preliminary observations are presented in the hope that they will stimulate further observations on this facet of lycaenid biology. Ants tending late instar larvae were collected at one locality in Washtenaw Co., in the vicinity of Embury Road (T1S R3E sect. 15), during 1977. Unless otherwise indicated, all identified ants are from this locality. The following summarizes our results.

Harkenclenus titus. Several late instar larvae were found feeding on the green fruits of *Prunus* sp. (possibly a hybrid between *P. serotina* Ehrh. and *P. virginiana* L.) (Rosaceae) on 22 May. Some were tended by *Formica subsericea* Say, and others by *Camponotus nearcticus* Emery. There are no previous reports of identified ants associated with this species.

Glaucopsyche lygdamas. The larvae of this species feed on the inflorescences of *Lathyrus venosus* Muhl., *Vicia caroliniana* Walt., and *V. villosa* Roth. (all Leguminosae) at various localities in Washtenaw Co. On 22 and 28 May, late instar larvae were found feeding on the flowers of *V. villosa*, an introduced species that occurs in open fields. Some of these larvae were tended by *Formica subsericea*, and others by an undetermined species of *Formica* in the *microgyna* or *rufa* species group.

Myrmecophily in this species was first noted by Brower (1911, Entomol. News 22: 359–363), but only Downey (1965, Entomol. News 56: 25–27) has identified ants involved. He found three species (*Formica comptula* Whlr., *Formica* sp. ? *rufa* group, and *Tapinoma sessile* (Say)) tending larvae feeding on *Lupinus argenteus* Pursh at one locality in South Dakota.

Celastrina argiolus. Females of the spring flight oviposit on the flower buds of sev-

eral species of shrubs that occur at the borders of marsh habitats. We have observed oviposition, and raised larvae to adults, on *Cornus alternifolia* L.f., *C. stolonifera* Michx. (Cornaceae), and *Viburnum lentago* L. (Caprifoliaceae). At one locality, both *C. stolonifera* and *V. lentago* grew together and were used by *C. ladon.* Larvae feeding on the young fruits of *C. alternifolia* on 29 May were tended by *Formica subsericea.*

Adults in subsequent flights of this species are much less common than in the spring, and we have only one hostplant record for these. In late July at Embury Road, females were ovipositing on the flower buds of a small herb, *Collinsonia canadensis* L. (Labiatae), which grows in the forest understory. On 9 August several mature larvae were noted feeding on the flowers of these plants. One was tended by two *Lasius alienus* Foerster, and another on a plant several meters away was tended by three *Camponotus nearcticus.*

In addition to the observations in Michigan, one of us (D.J.H.) observed *C. ladon* ovipositing on *Verbesina virginica* L. var. *virginica* (Compositae) at Florida Caverns State Park, Liberty Co., Florida, on 15 September 1976. A search of the inflorescences yielded several mature larvae being tended by *Crematogaster lineolatus* (Say), which also tended aphids on these plants.

An excellent account of the behavior of ants and larvae of *C. ladon* is given by Edwards (1878, Can. Ent. 10: 131–136), who reported that ants were "indifferent" to larvae feeding on *Cornus,* but that they "eagerly" tended those on *Cimicifuga racemosa.* However, in our experience, larvae are very attractive to ants regardless of the hostplant being used (whether *Cornus, Viburnum, Collinsonia,* or *Verbesina*). Clark (1936, Nat. Geog. Mag. 69: 679–692) gives the only previous record of an ant species associated with *C. ladon* in North America, *Crematogaster lineolatus.*

Although most of our data for these three lycaenids are limited to one locality, it is presumed that the association of their larvae with ants is opportunistic and dependent on the exploitation of the association by the ant. (The association may be more properly termed "lepidopterophily" on the part of the ant rather than myrmecophily on the part of the butterfly.) Each lycaenid was tended by several species of ants, and we suspect that further observations would reveal a greater number of ants associated with each of these in Washtenaw Co. In addition, *Formica subsericea* and *Camponotus nearcticus* (neither of which has been previously reported tending lycaenids (Downey, pers. comm.)) attended several of the lycaenids. This argues against a strict species to species relationship between ants and these larvae, although such relations often occur in the Old World (see Hinton, 1951, Proc. Soc. Lond. Entomol. Nat. Hist. Soc. 1949–1950, pp. 111–175). However, the report of pupae of *G. lygdamas* in an unidentified ant nest (Tilden, 1947, Pan-Pacific Entomol. 23: 42–43) suggests that more complex relations may occur in North America.

We would like to thank several people: Mary Talbot identified the Michigan ants, William F. Buren identified the Florida ants, and John C. Downey provided useful references and comments.

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EUPHYES BIMACULA (HESPERIIDAE) IN THE
SOUTHEASTERN COASTAL PLAIN

While studying the pollination ecology of *Zenobia pulverulenta* (Bartr. ex Willd.) Pollard (Ericaceae), a shrub endemic to the coastal plain of southeastern Virginia and the Carolinas, I collected a single male specimen of *Euphyes bimacula* (Grote and Robinson) in the Croatan National Forest approximately 13 km southeast of Maysville, Jones Co., North Carolina. The *Euphyes* was collected on 31 May 1978 at 1500 EDT while visiting flowers of *Zenobia*, presumably for nectar. The *Zenobia* was growing in an artificially created savannah bordered on the south and east by pocosin, the native semi-evergreen coastal bog vegetation of this area.

This specimen is one of the few documented southeastern coastal plain records for this skipper and supports Shapiro's (1971, J. Res. Lepid. 9: 125–155) description of the Great Lakes–Northern Coastal Plain, nondisjunct; Southern Coastal Plain, disjunct distribution of this species. *Euphyes bimacula* had long been considered a northern species. Both Klots (1951, A Field Guide to the Butterflies, Houghton Mifflin, Boston, Massachusetts) and MacNeill, in Howe (1975, The Butterflies of North America, Doubleday, Garden City, New Jersey) reported its range as New England and Ontario S to Virginia and W to Wisconsin, Iowa and Nebraska. Klots (1951, op. cit.) dismissed earlier records of more southern collections as misidentifications. Yet, when Shapiro (1971, op. cit.) mapped the distribution of *E. bimacula* he included three southeastern coastal plain records. These records were based upon a single collection from Mobile, Mobile Co., Alabama (Mather & Mather, 1958, Tulane Stud. Zool. 6: 63–109), a Southern Pines, Moore Co., North Carolina specimen in the United States National Museum and a Georgia collection which presumably is the same as the Blichton, Bryan Co., Georgia collections discussed in more detail by Harris (1972, Butterflies of Georgia, Univ. Okla. Pr., Norman, Oklahoma). Since then Gatrelle (1971, J. Lepid. Soc. 25: 143; 1975, ibid. 29: 56–59) has added Summerville, Berkeley Co., South Carolina to the list of southeastern coastal plain localities where *E. bimacula* has been collected.

Apparently little is known about the biology of *Euphyes bimacula*. Both Klots (1951, op. cit.) and MacNeill, in Howe (1975, op. cit.) noted this skipper's preference for wet habitats, particularly bogs, swamps and marshy meadows. The Jones Co., North Carolina and the Bryan Co., Georgia specimens (Harris, 1972, op. cit.) were taken in wet habitats. The latter specimens were collected on flowers of pickerel weed [*Pontederia cordata* L.], which is aquatic. Presumably, the Moore Co., North Carolina, South Carolina and Alabama collections were also made in wet habitats. Although Klots (1951, op. cit.) and MacNeill, in Howe (1975, op. cit.) both report that *Euphyes bimacula* flies in July, there are reports of its flying from late June to early September (Price & Shull, 1969, J. Lepid. Soc. 23: 186–188). The South Carolina specimens were taken in July (Gatrelle, 1971, op. cit.). It is interesting to note, however, that the Jones Co., North Carolina and the Georgia collections were made in May. This suggests that *E. bimacula* flies earlier in the southern portion of its range. Unfortunately I have no information as to when the Alabama and Moore Co., North Carolina collections were made.

Continued collecting in suitable habitats in the southeastern coastal plain should yield additional records of the two-spotted skipper, *Euphyes bimacula*. Collections from the coastal plain of Virginia, Maryland and Delaware would lend further credence to Shapiro's (1971, op. cit.) hypothesis that *E. bimacula* was displaced far to the south during the Pleistocene and has since migrated back north along the Atlantic Coastal Plain and then west to the Great Lakes.

Forest Service for permission to collect in the Croatan National Forest. The *Euphyes* has been deposited in the United States National Musuem.

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NOTICE TO THE MEMBERSHIP FROM THE RETIRING EDITOR

Three years have brought about a number of changes in the Editorship. One of the foremost of these has been the increased costs of publication incurred by the *Journal*. During the coming years I can foresee a reduction in the amount of material which the Society will be able to publish, as a result of increasing inflationary costs. Recently, we have experienced delays in issuing Vol. 34, issues 3 and 4, which in part resulted from the financial bind in which the Society now finds itself.

The editorship has been a continual learning experience for me. Contributors must realize that the editor, his associates, and his reviewers give generously of their time and efforts, in order to bring the readers a *Journal* of high quality. The workload is tremendous, and the logistics of accomplishing the review of submitted papers on an annual basis soon becomes a continuous, unending task. During the past three years 370 articles, general notes, obituaries, and book reviews have been processed by the editors. Each manuscript presents its own difficulties and idiosyncracies, some of which have not been previously encountered.

Contributors can help ease the difficulties encountered by the editorial staff of the *Journal* by making certain that all submitted manuscripts are of the highest quality possible. Before submitting papers, authors should have others critically read them, and make constructive suggestions for their improvement. Once this has been done, the *Journal* requirements should be closely followed while preparing the final copies.

I apologize to the readership for the lateness of the November issues during the past three years. This has resulted in part from compilation of a more complete indexing of the genera and species contained in each volume. Such an index cannot be completed and type-set, until after the page proofs of the last quarterly issue have been received.

I wish to thank especially those people who have helped ease my editorial burdens by shouldering some of the responsibilities themselves. Dr. Frances S. Chew has worked tirelessly as Managing Editor of the *Journal* for the past two and a half years. Dr. D. C. Ferguson and Dr. T. D. Sargent have served as Associate Editors, and both have reviewed a heavy load of manuscripts for the *Journal*. Others whose names appeared in Vol. 33, No. 4, have generously supported the *Journal* by providing critical manuscript reviews at the editor's request. Dr. Lee D. Miller and Dr. Jaqueline Y. Miller both worked long and hard soliciting, and initially screening most of the manuscripts contained in the Harry Clench Memorial issue, which was edited with help from Dr. Robert Robbins. Barbara L. Phillips, a work study student at UMBC, has handled most of the manuscript correspondence typing chores while I have served as editor, and she has worked diligently preparing the annual indices, as well. Finally, the personnel at Allen Press, Inc. have been very helpful to all of us, and have turned out the high quality *Journal* copies which the membership receives.

At this point in time the editorship passes to Dr. Thomas D. Eichlin, Bureau of Entomology, California Department of Food and Agriculture, 1220 "N" Street, Sacramento, California 95814. The transfer of the *Journal* files to him is already underway. To Tom and his staff workers we extend our heartiest congratulations on his appointment to the editorship, and wish him good luck and success during his tenure as editor of the *Journal*.

AUSTIN P. PLATT, Retiring Editor, *Department of Biological Sciences, University of Maryland Baltimore County, 5401 Wilkens Avenue, Baltimore, Maryland 21228.*

BOOK REVIEWS

Ten Years of "Microlepidoptera Palaearctica"

During a meeting of Bavarian entomologists in Munich in 1958, a discussion occurred regarding investigations of the Microlepidoptera. In the presence of Dr. G. Petersen (Berlin) and myself, Dr. H. J. Hannemann (Berlin) expressed his opinion that a new revised edition of the now quite obsolete Rebel (1901) catalogue was much needed. I said that the situation could not be solved by editing the catalogue, but that we should consider publishing a modern revision of this group, covering the Palaearctic Region, and applying a holistic approach.

I have thought about this idea ever since, and after two decades, I refer to this discussion as the hour at which the "MP" was conceived, although the period required to produce the work in its final form lasted another seven years. The first volume was completed in 1965. The significance of the work, however, became evident only after the first three volumes had appeared. These included 2135 text pages, 105 color plates, 465 ink drawing plates, and covered a total of 1052 species, including 284 synonyms, with descriptions of 126 species and 11 genera new to science. At present, treatments of the Crambinae, Ethmiidae, Cochylinae, trifine Acrobasinae, and Lecithoceridae are available.

The concept of this work was first presented to lepidopterists at the International Congress of Entomology in Vienna in 1960. Eighteen theses supporting the work were accepted and adopted as taxonomic studies by a number of periodicals.

The complicated background through which the work originated remains obscure. Even P. C. Zeller, perhaps the most outstanding lepidopterist of the past century, left behind 11 synonyms in the single subfamily Crambinae. Thus, a mere revision of Rebel's catalogue never would have led to the goals which we resolved to attain through our work.

I was aware from the very beginning that such a magnificent project hinges on finding a satisfactory publisher. The question was, could we find one who would realize that business and profit are not the primary goals when a work of this kind is to be undertaken? My doubts were realized when negotiations with the Schweizerbartscher Verlag in Stuttgart fell through because of the publisher's disproportionate financial demands. By accident my project attracted the attention of a representative of the Badische Anilin-und Sodafabrik (BASF), in Ludwigshafen, with whom I had been meeting when I was in Berlin. Through his influence, I gained access to Mr. Kurt Schäfer, business director of the BASF, a highly cultured person. Schäfer had spent three full decades in Shanghai where he met Hermann Höne, the famous organizer of lepidopteran expeditions to China. Schäfer and I agreed in our admiration for the works of Goethe and Busch.

Of course, Schäfer himself was not the one who would ultimately decide upon the support of my project. That was up to Professor Wurster, director general of the BASF. But Schäfer was Wurster's right-hand man. Wurster had important contacts (he was, for instance, a member of the board of the Deutsche Bank, the Volkeswagen-Stiftung, and the Germanische National-Museum in Nuremberg). He was also a member of the central committee of the Deutsche Forschungs-Gemeinschaft (DFG), which was principally sponsored by the BASF. My meeting with Professor Wurster was far from smooth at first. It was not easy to win over such a business manager to a project of this kind. Fortunately, we found a precious agreement in our musical interests. Yet the battle was still not won. What decided it was the visit which both gentlemen paid to our collections at the Landessammlugen fur Naturkunde, in Karlsruhe. Here it was Nature itself that prevailed: I demonstrated, using a binocular lens, some representatives of the genera *Cosmopterix*, *Lithocolletis*, *Adela*, *Orneodes*, etc., the splendour of which so impressed both gentlemen that they no longer hesitated in making their decision.

Under these circumstances, I felt obliged to express my sincerest gratitude to them, which prompted me to name the splendid species *Euplocamus schaeferi* and *Ethmia wursteri* in their honor.

The critical moment, however, appears to have been the visit to Professor Hesse, president of the DFG, to whom I had gained access through Wurster. I not only handed Professor Hesse my application, but also answered his numerous questions. The debate in the presidium of the DFG, however, developed unfavorably and, still, before the final vote, it was decided not to recommend publication of the work. Here, it seems, a freak occurrence came to our assistance again; at that moment, one of the members of the presidium uttered the following remark, "What would your decision be if the proposer's name did not spell Amsel but Linnaeus?". In the ensuing vote, my proposal was accepted unanimously. Thus the DFG assumed responsibility for the economic aspects of the project.

The next problem was that of finding a suitable publisher. After my attempt in Stuttgart fell through, an idea occurred to me during my short holiday in the Tyrol that the person needed should be an entomologist. I left the Tyrol directly for Vienna, where, after years of previous intensive correspondence and developing friendship, I finally met with Hans Reisser. Reisser was an outstanding lepidopterist and editor of a significant lepidopteran periodical in Austria. He also belonged to the Reisser dynasty of printers and, moreover, his word was of great weight with the printers Fromme & Co. Reisser was a man of outstanding organizing ability, exceptional scope of knowledge, and unique personal charm and culture. He became just as enthusiastic about the idea as I was.

What remained now was to find an artist would would agree to undertake the illustrations. Long before the definitive "yes" was given by the DFG, I had been exchanging letters with Dr. Frantisek Gregor, whose color illustrations, accompanying his own lepidopteran papers, had attracted my attention for many years. Gregor is an exceptionally talented man, although particularly shy and modest, but it was evident (to us, as well as to him) that he would be the one to take over this task of extraordinary importance. Dr. D. Povoiny, Gregor's intimate friend, engaged him in passionate debates along these lines. I wanted to see that a work as extensive as the "MP" be adequately carried through to completion. Gregor provided both the precision of a scientist and the singular talent of an artist. Today, after many years, it is clear that Gregor's artistry is comparable to that of both Robinson and Culot. Now, Gregor's talents have become known on an international scale. To date, he has painted some 2000 color illustrations for the "MP."

Let us consider again the personality of Hans Reisser. It is his devotion to the idea, and his organising ability, as well as his splendid skill in translating, and other indefinable attitudes involving the project, to which the work owes its final realization.

Reisser, Schäfer and Wurster have passed away, as have other persons who did not contribute directly to the "MP," such as Dr. S. Obrazcov, Professor Dr. G. de Lattin, and Dr. Graf v. Toll, but who supported the work with their authority. In fact, their work contributed to the knowledge of the groups being elaborated for the "MP." During the past years we established an editorial committee including the late Hans Reisser, Professor Sauter (Zurich), Dr. U. Roesler (Karlsruhe), as well as myself. Dr. U. Roesler is expected to take over as my successor when I step down.

There may be different opinions concerning the concept of the work. 1) One may argue that the present knowledge of Microlepidoptera of the Palaearctic Region is too incomplete (due to the inaccessibility of many regions) to be supported by sufficient material, that 2) specialists are not available for all groups, and that 3) the volumes have not been issued in systematic order.

Such objections are spurious, considering the immense publicity of a similar well-known and useful work, Lindner's "Fliegen der Palaarktischen Region," which deals with the Diptera. The order in which the various volumes of "MP" are issued depends on the time and energy which the different authors have to devote to the project, the degree to which the various taxonomic groups are known, and the availability of material.

Our prior experience suggests that future individual volumes should not cover more than a maximum number of 250 species. Certainly, even the question of the price of a single volume cannot be overlooked. This problem is entirely out of the hands of the editors. It is set by the publisher and the sponsor, that is, the DFG. Ever since the first volume was issued, 500 subscription copies have been produced. Even such a voluminous book as Part Four (which is a double volume) has received wide publicity.

The authors for all of the future volumes have been arranged. We have been trying to provide extra help for Gregor, the only illustrator of the work so far, whose outstanding performance to date must not be allowed to suffer from time shortage or other future stresses. Therefore, under Gregor's guidance, our colleague Zawada (Cracow) obtained the necessary training for illustrating some of the groups.

On the tenth anniversary of the "MP," we may state, with satisfaction, that our work is a success. Such a major work requires both great personalities and an exceptionally favorable constellation. In other words, to produce such magnificent volumes requires both talented people and the proper conditions under which they can work. This has been accomplished by complying with the words of Nietzsche: "I love people who can give away themselves." The "MP" has been lucky in having found such people, and because of this I believe that we shall eventually succeed in completing this great work.

H. G. Amsel, *Landessammlungen für Naturkunde Karlsruhe, D75 Karlsruhe 1, Erbprinzstrasse 13, Postfach 4045, Karlsruhe, West Germany.*

Butterflies of the Australian Region, second ed., by Bernard D'Abrera. 1977. Lansdowne Press, Melbourne, Australia. 415 pp., many illustrations. Available exclusively in North America through Entomological Reprint Specialists, P.O. Box 77224, Dockweiler Station, Los Angeles, California 90007. Price $87.50 (U.S.).

When I reviewed the first edition of this book in these pages some years ago, I waxed rather poetic in my praise of it. I regret to say that I cannot be so enthusiastic about the revised edition. The promotional material that preceded the volume suggested that substantial modifications of the text and illustrations would make this book as indispensable to the students of Australian regional butterflies as was the first—implying that the first edition would become obsolete. With few exceptions, notably the treatment of the Lycaenidae, such has not been the case.

The illustrations have not essentially changed since the first edition (to be sure, there are a few additions and deletions), and while the illustrations are still very good (the best available), my feeling is that the printing is not as good as it was in the first edition, nor are the colors as true-to-life. Perhaps the shortcomings here may be attributed to the use of the same, apparently now tired, plate blocks.

The most important contribution in this book is the complete revision of the section on the Lycaenidae based on Eliot's excellent 1973 higher classification of the group. One can only wish that other families had been so revised. A few species accounts have been rewritten to comply with revisions published (chiefly in England) since the publication of the first edition. These include rewritings on *Ornithoptera goliath*

(many "subspecies" relegated to forms), *Vindula* (*dejone* now accepted as a valid species name, rather than *erota*, although on p. 203 the subspecies *ricussa* Fruhstorfer is still listed as an *erota* subspecies, probably because the copy on that page was not changed), and, of course, almost the entire lycaenid section. A number of entities not included in the first edition, such as *Charaxes mars madensis* Staudinger (p. 247), *Austroypthima petersi* Holloway (p. 265), *Paratisiphone lyrnessa* (Hewitson) (p. 277) and *Stilbon meeki* Rothschild and Jordan (p. 301), are described in detail and photographed in their proper positions within the book.

Other names overlooked in 1971 are included, usually just as names with associated ranges. The discrimination of these subspecies (mostly) is presumably based on label data, rather than discernable morphological characteristics. The editors may have decided to cut the characters from the text, but the impression remains that simply because a name refers to a population on a different island, it must be retained as "real," and that it must be biologically significant.

A number of new names are proposed in the text, and this factor alone will make the book a must for both bibliophile and taxonomist alike. Personally, I feel that if new names are the only reason for buying a book, we are getting shortchanged. The book should be something we want, not something that we must have. These names could better have been proposed in a journal prior to their validation in a book—journals are usually far less than $87.50!

A new section was added ("On Photographing Butterflies"), a philosophical piece that gives little information and adds nothing to the book. These pages were better utilized in the 1971 edition, where they contained a glossary. The rewritten section on classification (p. 30) may or may not be clearer than it was in the first edition, but the misspelling of Libytheidae (as "Lybitheidae") is perpetuated.

Additional foodplant information is tipped into the manuscript throughout the book, and this in company with the rewritten lycaenid section are the most valuable revisions of the present volume.

I must confess to having mixed emotions not only about this book, but also about the projected further volumes dealing with other world fauna. If there are so many incomplete parts of D'Abrera's home fauna in this book, one must shudder to think what might happen when he tackles a strange area's butterflies, such as the Neotropics (projected in one volume). If the reader has no interest in Lycaenidae (yes, there are a few!) and has the 1971 edition, I would not suggest he also pick up this one. If he does not have a book on the Australian region's species the present book is the best available. If he has the first edition, is interested in taxonomy and wants to stay abreast of at least *most* of the nomenclature, then, like it or not, he must have this book and be prepared to complain loudly about the price. I regret to say that I fall into the latter category!

LEE D. MILLER, *Allyn Museum of Entomology, 3701 Bay Shore Road, Sarasota, Florida 33580.*

INDEX TO VOLUME 34
(New names in **boldface**)

PLANT INDEX FOR VOLUME 34

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of the collection and study of Lepidoptera. Contributors should prepare manuscripts according to the following instructions.

Abstract: A brief abstract should precede the text of all articles.

Text: Manuscripts should be submitted in *triplicate*, and must be typewritten, *entirely double-spaced*, employing wide margins, on one side only of white, 8½ × 11 inch paper. Titles should be explicit and descriptive of the article's content, including the family name of the subject, but must be kept as short as possible. The first mention of a plant or animal in the text should include the *full scientific name*, with *authors* of zoological names. Insect measurements should be given in *metric units*; times should be given in terms of the *24-hour clock* (e.g. 0930, not 9:30 AM). Underline only where *italics* are intended. References to footnotes should be numbered consecutively, and the footnotes typed on a separate sheet.

Literature Cited: References in the text of articles should be given as, Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and all must be listed alphabetically under the heading LITERATURE CITED, in the following format:

SHEPPARD, P. M. 1959. Natural selection and heredity. 2nd. ed. Hutchinson, London. 209 pp.

———— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10: 165–216.

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of the

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Cover Illustration: Adult male *Anthocharis sara* Lucas (Pieridae) on inflorescence of fiddleneck (*Amsinckia intermedia* Fischer & Meyer, Boraginaceae). These butterflies occur in central Arizona during spring, often flying through small canyons and washes. Their larvae feed on a wide variety of mustards (Cruciferae). Original drawing by Dr. Rosser W. Garrison, Calle Iris UU18B, Rio Piedras, Puerto Rico 00926.

HYBRIDIZATION OF *SATURNIA MENDOCINO* AND *S. WALTERORUM*, AND PHYLOGENETIC NOTES ON *SATURNIA* AND *AGAPEMA* (SATURNIIDAE)

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ABSTRACT. The taxonomic relationship of *Saturnia walterorum* and *S. mendocino* is discussed in terms of laboratory hybrids, larval morphology, comparative life history, and phenetics of intermediate populations. Results indicate that these moths represent different taxa, but are best described as semispecies. The two taxa freely interbreed in the laboratory. Hybrid F_1 females with *walterorum* as the female parent had normal fertility and fecundity; females from the reciprocal cross were viable but sterile. The two taxa are very similar morphologically and differ mainly in the dimorphic female of *walterorum*. Populations in the southern California Coast Ranges may represent intergrades. A discussion of the phylogeny of the endemic California *Saturnia* and the closely related *Agapema* stresses the coevolution of these moths and their sclerophyllous host plants in response to historic climatic changes.

In the New World, the genus *Saturnia* consists of three species whose distribution is centered in California. The three species, *Saturnia walterorum* Hogue & Johnson, *S. mendocino* Behrens, and *S. albofasciata* (Johnson), exhibit life history characteristics which are adaptations to utilizing sclerophyllous food plants in a Mediterranean climate of winter rains and summer drought. The localized populations of these moths, their rapid and erratic flight, and the rugged terrain they inhabit, make them difficult to collect. As a result, complete and accurate life history descriptions are lacking for all three species. In this paper we examine the taxonomic relationship of *S. walterorum* and *S. mendocino* in terms of laboratory hybrids, comparative life histories, larval and adult phenotypes, and phenetics of

geographically intermediate populations. We extend our discussion to include a proposed phylogenetic scheme which includes the closely related genus *Agapema*, based on biogeographic and geofloral data.

Methods

In an effort to understand the genetic relationship between *Saturnia walterorum* and *S. mendocino*, we began hybridization studies in 1974. Our *walterorum* stock was from Dictionary Hill, Spring Valley, San Diego Co., Calif., while the *mendocino* used in the study came from Thompson Canyon, near Lake Berryessa, Yolo Co., California. A large series of wild and reared adults from each location was examined, and characters which represent diagnostic differences between the two species were sought. We selected six characters which could be either measured or scored as to presence or absence: forewing length, dorsal forewing and hindwing discal eyespot length, the ratio in length between the forewing and hindwing discal eyespot, the presence or absence in males of a white apical patch of scales on the ventral surface of the forewing, and the presence or absence of a bold submarginal black band on the dorsal forewing surface of females.

Larvae secured during the study were reared outdoors in screen cages after the first instar on fresh branches of *Arctostaphylos* spp. maintained in water. Most larvae pupated by June, and began to emerge the following year during February or March. Cage matings were easily obtained, usually within minutes after the female began "calling." Mated females oviposited readily in paper bags or other containers in the absence of food plant.

The fecundity of each female was determined by measuring the number, size, and batch weight of the eggs. The degree of fertility was based on the number of eggs which hatched within each batch. In the field, males were obtained by means of funnel traps or wire cages each containing a virgin female. In this way we were able to sample populations more efficiently than searching for larvae or adults.

Results

In order to interpret the phenotypes of hybrid specimens we estimated the range of variation in the parental populations. The right forewing length of male *walterorum* averaged just over 11 percent greater than that of male *mendocino*, while that of female *walterorum* was 18 percent greater than female *mendocino* (Table 1). A t-test indicated that the difference in wing length between the two species

TABLE 1. Phenotypic data for S. walterorum, S. mendocino and their hybrids.

| | FEMALES | | | | | MALES | | | | | |
| | Eyespot | | ratio | F-wing length | Sbm. band | F-wing | Eyespot | ratio | F-wing length | Apical spot | n^3 ♀/♂ |
	F-wing	H-wing					H-wing				
a. mendocino	3.70[1] / 0.40	3.81 / 0.41	0.97	32.84 / 1.75	no	2.60 / 0.30	2.73 / 0.35	0.95	27.07 / 1.11	no	21/43
b. ♂ F_{1a} hybrid × ♀ mendocino	4.71 / 0.24	4.82 / 0.23	0.98	33.11 / 0.54	no[2]	3.78 / 0.26	3.63 / 0.24	1.04	28.14 / 0.54	no	12/18
c. ♂ walterorum × ♀ mendocino = F_{1a}	5.33 / 0.39	5.63 / 0.31	0.95	37.20 / 2.42	yes	3.48 / 0.21	3.75 / 0.47	0.93	29.43 / 1.96	no	18/18
d. ♂ F_{1a} hybrid × ♀ F_{1a} hybrid	—	—	—	—	—	3.41	3.80	0.90	28.20	no	0/1
e. ♂ F_{1b} hybrid × ♀ F_{1b} hybrid	5.33	4.33	1.23	32.00	no[2]	3.55	3.00	1.18	27.00	yes	3/2
f. ♂ mendocino × ♀ walterorum = F_{1b}	5.55 / 0.33	5.24 / 0.25	1.06	34.93	no[2]	4.23 / 0.42	3.81 / 0.39	1.11	28.18 / 1.00	no	10/12
g. ♂ F_{1a} hybrid × ♀ walterorum	6.23 / 0.62	6.02 / 0.32	1.04	37.08	yes	4.17 / 0.26	3.81 / 0.31	1.09	28.80 / 1.92	yes	11/12
h. walterorum	7.34 / 0.55	6.28 / 0.46	1.17	40.33 / 1.64	yes	4.25 / 0.40	4.08 / 0.44	1.04	30.52 / 1.27	yes	13/16

[1] Measurements in mm with S.D. given below.
[2] Some females showed a trace of submarginal band.
[3] Sex ratio based on undamaged, measured specimens. Complete data for b not available. Hybrid sex ratios do not differ significantly from expected 1:1.

TABLE 2. Fecundity and fertility of S. walterorum, S. mendocino and their hybrids.

| | Cross | No. ova laid | Ova length | | Avg. ova wt. g | % hatch |
			mm	S.D.		
a.	♀ walterorum	114	2.44	0.06	0.0035	97.0
b.	♀ mendocino	83	2.47	0.07	0.0037	96.4
c.	♂ walterorum × ♀ mendocino = F₁ₐ	77	2.47	0.07	0.0037	97.5
d.	♂ F₁ₐ hybrid × ♀ mendocino	73	2.47	0.07	0.0037	87.8
e.	♂ F₁ₐ hybrid × ♀ walterorum	137	2.24	0.07	0.0034	91.5
f.	♂ F₁ₐ hybrid × ♀ F₁ₐ hybrid	33	1.79	0.69	0.0025	3.3
g.	♂ walterorum × ♀ F₁ₐ hybrid	52	1.75	0.68	0.0017	0.0
h.	♂ mendocino × ♀ F₁ₐ hybrid	44	1.92	0.18	0.0022	0.0
i.	♂ mendocino × ♀ walterorum = F₁ᵦ	130	2.47	0.05	0.0036	96.0
j.	♂ F₁ᵦ hybrid × ♀ F₁ᵦ hybrid	96	2.14	0.01	0.0036	98.0
k.	(♂ F₁ₐ hybrid × ♀ walterorum)2	73	2.10	0.09	0.0037	96.7
l.	(♂ F₁ₐ hybrid × ♀ mendocino)2	75	2.21	0.16	0.0032	0.0

and both sexes is significant (P < .05). The eyespots on the dorsal fore-wing and hindwing are about twice as large in *walterorum* as in *mendocino*. In *walterorum*, the forewing eyespot is larger than the hindwing eyespot, while in *mendocino* the opposite is true. Thus the ratio of the forewing to hindwing eyespot is greater than 1 in *walterorum*, and less than 1 in *mendocino*. This character was scored qual-itatively and not treated statistically. As with wing length, the larger discal eyespot size of male and female *walterorum* are significantly greater than those of *mendocino* (P < .05). Analysis indicated that only 10 percent of the difference in eyespot size is attributed to the difference in wing length between the two species. Considering the few characters available, a hybrid index was not deemed neces-sary. In terms of qualitative differences, all male *walterorum* have a distinct white apical patch about 2 mm long, on both surfaces of the forewing. Males of *mendocino* may have a similar, but smaller white apical patch on the dorsal surface only, thus the presence or absence of the white apical patch on the ventral surface is diagnostic. Finally, all female *walterorum* have a bold submarginal black band on both the dorsal and ventral surface of the forewing, which is lack-ing in female *mendocino* (Table 1a, h).

The average egg weight and length of both *walterorum* and *men-docino* is similar (ca. 0.0036 g, 2.46 mm, Table 2). One way analysis of variance combined with a Duncan multiple range was used to compare both egg weight and length. Although no difference was found between *walterorum* and *mendocino* ova, a statistically signif-icant difference in average egg weight and length was found between F₁ₐ ova and both parental species (P < .05) (Table 2a, b, f, g, h). Female *mendocino* usually deposit 70 to 80 eggs within 5 or 6 hours
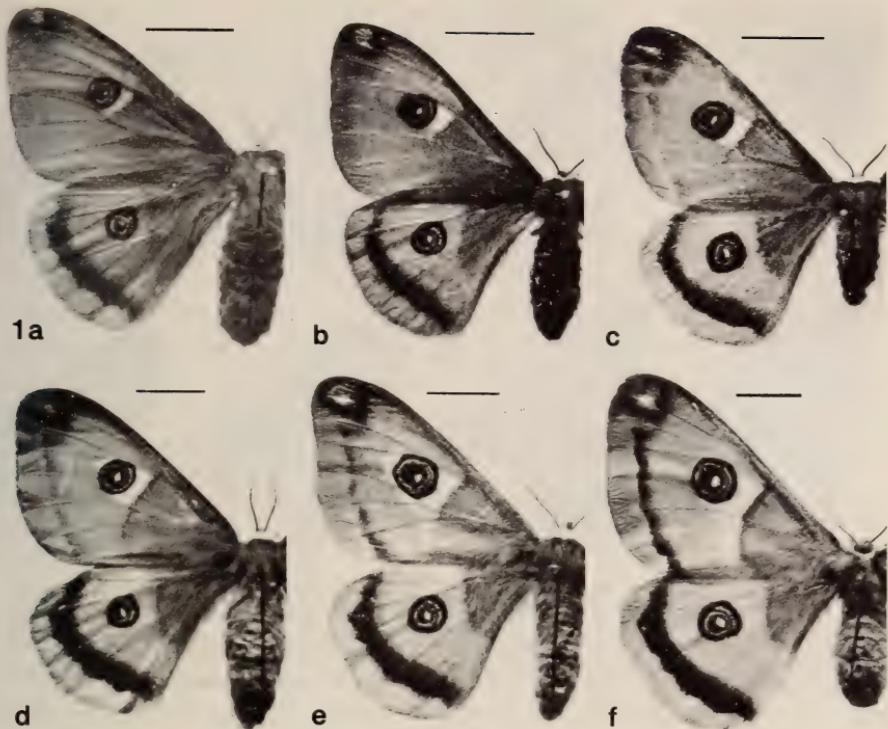
FIG. 1a–f. Female *Saturnia* and hybrids. **1a,** S. *mendocino;* **1b,** ♂ F_{1a} × ♀ *mendocino;* **1c,** ♂ *walterorum* × ♀ *mendocino* = F_{1a}; **1d,** ♂ *mendocino* × ♀ *walterorum* = F_{1b}; **1e,** ♂ F_{1a} × ♀ *walterorum;* **1f,** S. *walterorum.* Black lines represent 10 mm.

after mating, while *walterorum* females deposit 100 to 140 eggs. The average fertility of each species was near 97 percent.

Table 1 presents phenotypic data on the hybrids that were produced under controlled conditions. The initial mating of a male *walterorum* to a female *mendocino* produced the F_{1a} hybrids, which were nearer in size to *walterorum* than *mendocino.* Hybrid F_{1a} females also had a distinct submarginal band which was not as well developed as that of typical *walterorum* (Table 1c; Figure 1c). The forewing to hindwing eyespot ratio of these hybrids was <1 as in *mendocino.* The F_{1a} hybrids also resembled *mendocino* in the appearance of the male apical spot (Table 1c). When the F_{1a} male was backcrossed to a female *mendocino,* the resulting adults were almost identical to typical *mendocino,* but the male eyespot ratio was equal to that of *walterorum* even though the eyespot size was greatly reduced relative to *walterorum.* Females lacked the submarginal band, and expressed an eyespot ratio similar to *mendocino,* although the absolute size of the spots
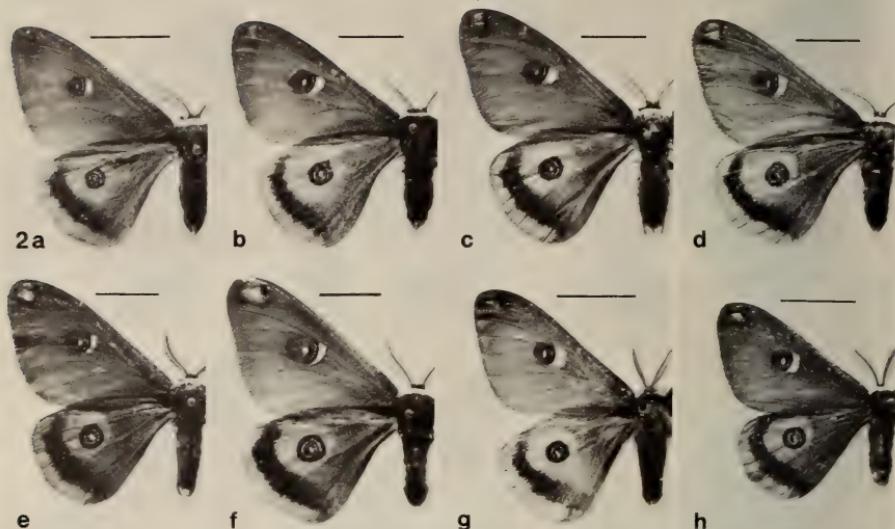
FIG. 2a–h.   Male *Saturnia* and hybrids. **2a,** S. *mendocino;* **2b,** ♂ F$_{1a}$ × ♀ *mendocino;* **2c,** ♂ *walterorum* × ♀ *mendocino* = F$_{1a}$; **2d,** ♂ *mendocino* × ♀ *walterorum* = F$_{1b}$; **2e,** ♂ F$_{1a}$ × ♀ *walterorum;* **2f,** S. *walterorum;* **2g,** Wild specimen, Cone Peak, Monterey Co.; **2h,** Wild specimen, La Panza, San Luis Obispo Co. Black lines represent 10 mm.

were larger. The F$_{1a}$ male backcrossed to a female *walterorum* produced progeny which expressed all of the qualitative characters associated with *walterorum,* while the quantitative characters were intermediate (Table 1e). In both backcrosses of F$_{1a}$ males to the parent species, the fertility was 6 to 9 percent below normal (Table 2d, e).

Unlike F$_{1a}$ males, the F$_{1a}$ females were almost totally sterile, and laid about half the normal number of ova. The eggs which these hybrid females produced were small, and of unusual shape and size, with an average weight of only 50–65 percent of normal (Table 2f, g, h). Dissection revealed some eggs contained dead, partially formed larvae, but the majority of the eggs lacked any observable embryonic development. Of the 96 eggs resulting from backcrosses to male *walterorum* and *mendocino,* none was fertile.

The progeny from the reciprocal cross, ♂ *mendocino* × ♀ *walterorum,* were the F$_{1b}$ hybrids. The F$_{1b}$ adults were similar in size to *mendocino,* and lacked the apical patch in the males, and submarginal bands in females. The eyespot size and ratio was intermediate in the females, while in the males the eyespot ratio was close to that of *walterorum.* Unlike F$_{1a}$ females, F$_{1b}$ females were fertile, producing the normal weight and number of eggs (Table 2j). When the F$_{1b}$ adults

were selfed, the resulting F_2 larvae were subvital and only seven were reared to adults. Of the five females, two emerged with crippled wings, two had thinly scaled wings and one appeared normal; the two males were normal.

The fertility and fecundity of the backcross progeny were tested by selfing (Table 2k, l). The ova size and weight were near normal for both crosses. The percent hatch was normal for the ova laid by the female whose female parent was *walterorum*, but none of the eggs hatched in the backcross with a *mendocino* parent. This may have been the result either of the pair separating prematurely or sterility.

In the pure stock of *mendocino* and *walterorum* the immature larval phenotypes, though very similar, are discrete and non-overlapping. Larvae from any given hybrid cross could express phenotypes of either species, as well as any number of intermediate forms. Thus, there was no clear case of phenotypic dominance. Mature larvae of each species can best be distinguished by differences in setal pattern and length (Tuskes, 1976).

DISCUSSION

Much of the biological information regarding the life history of the New World *Saturnia* was summarized by Ferguson (1972), but not all of the published information available at the time was correct. In describing *mendocino*, Behrens (1896) gave the type locality as "the forests of Sequoia Sempervirens, of the Coast range of Mendocino County, Cal." Thus, Ferguson (1972) contrasted the "moist coniferous forest" inhabited by *mendocino*, to the arid chaparral habitat of *walterorum* in southern California, and implied that this ecological distinction might be diagnostic. In fact, *mendocino* occurs in the arid Oak-Digger Pine woodland, and chaparral plant communities, where it feeds on manzanita, *Arctostaphylos* spp. (Ericaceae). Though these plant communities may occur adjacent to coastal or canyon redwood forests, the ecological and climatological differences are severe (Bakker, 1971; Major, 1977). In addition to manzanita, there is one report (Tilden, 1945) of *mendocino* larvae feeding on Madrone, *Arbutus menziesii* Pursh (Ericaceae), which on occasion is found in drier areas along the border of the redwood community, and opens the possibility that *mendocino* may occur there.

Saturnia mendocino occurs in the western foothills of the Sierra Nevada, from Tulare Co., north into the Cascade range of Siskiyou Co. (Fig. 3). One specimen has been collected just north of the California border in Jackson Co., Oregon (Tuskes, 1976), and marks the northern limit of well defined chaparral communities; whether *mendocino* occurs farther north on *Arctostaphylos* or possibly *Arbutus*
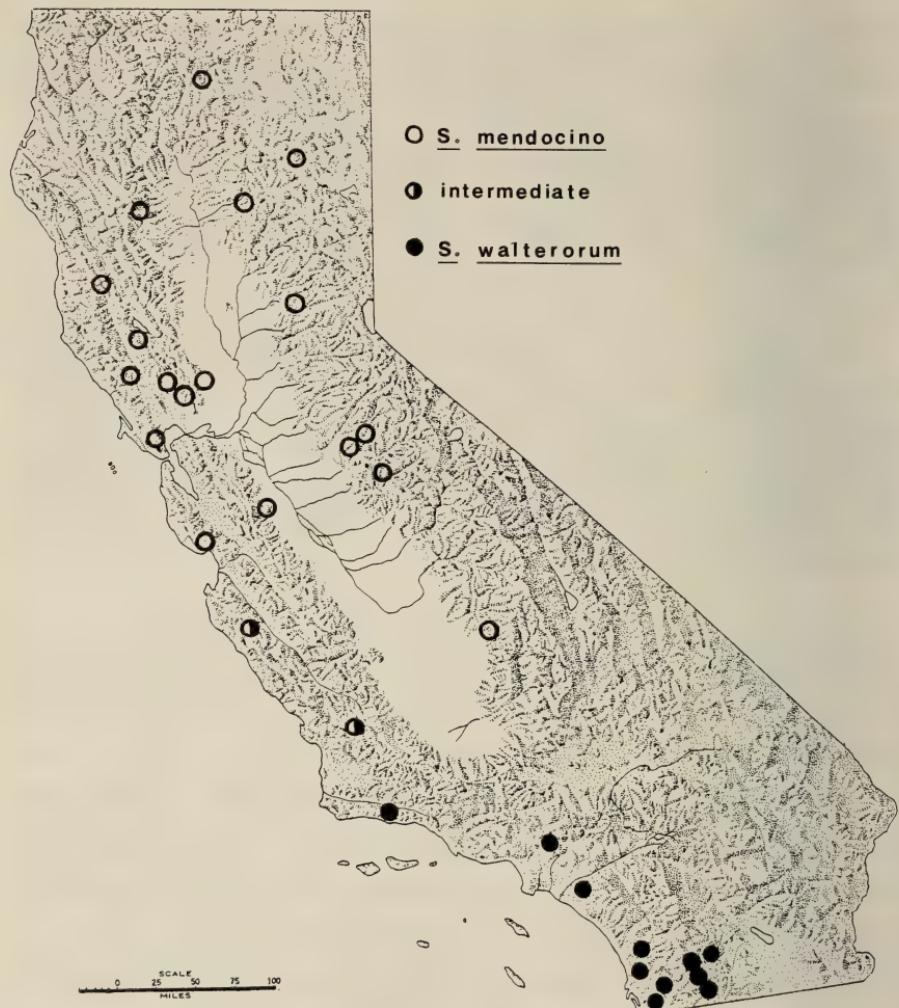
FIG. 3. The known distribution of *S. walterorum* and *S. mendocino* in California.

remains to be determined. The southern limits of *mendocino* in the Coast Range have not been adequately determined. Specimens with intermediate phenotypes have been collected in Monterey and San Luis Obispo Counties, and will be discussed later. *Saturnia walterorum* is found from Santa Barbara Co. south to San Diego Co. and undoubtedly occurs in Baja California. Though *walterorum* is not reported from Riverside or San Bernardino Counties, suitable habitat for it occurs in both counties. In the coastal chaparral community, *walterorum* is associated with *Rhus laurina* Nutt. and *Rhus integri-*

folia Benth. & Hook. (Anacardiaceae) while above 1300 m the larval host is *Arctostaphylos* (Tuskes, 1974).

The flight time for both species is generally from February to April, depending on altitude and seasonal differences. Populations of *mendocino* in the Cascade Range, of those of *walterorum* in the Laguna Mts. at 2600 m may not emerge until April or early June. The emergence of adults appears to be highly synchronized, and occurs during the first few days of warm weather following a protracted cool period. The pupae of both *walterorum* and *mendocino* possess a patch of clear integument over the brain which suggests that daylength may act as a cue controlling development as has been demonstrated in *Antheraea polyphemus* and *A. pernyi* (Williams & Adkisson, 1964) and *Actias* (Miyata, 1974). Whether this mechanism in *Saturnia* initiates development in the spring or controls summer diapause, or both remains to be determined.

Sala & Hogue (1958) mention the development of definable adult structures, such as wings and legs in the pupa during early autumn and state further that no *walterorum* pupae remained viable longer than one year. We have not found the development of the pupa to be different from other North American saturniids. In addition, we found that both *mendocino* and *walterorum* are capable of surviving at least two years in the pupal stage. Differences in pupal development and the ability to survive more than a year in the pupal stage may be the result of different rearing conditions.

The third American species in this genus, *S. albofasciata*, is unique when compared to the other two. The adults of this species exhibit strong sexual dimorphism, and fly during October and November, rather than the spring. Male *albofasciata* fly and mate in the late afternoon, while females oviposit within a few hours after sunset. The larvae feed on *Ceanothus* (Rhamnaceae) and *Cercocarpus* (Rosaceae). *Saturnia albofasciata* occurs in both the Coast Range and the foothills of the Sierra Nevada from Lake Co. south to Los Angeles Co. (Ferguson, 1972). Recently specimens have been taken near Julian and Campo in San Diego Co., and this species probably occurs in northern Baja California. Additional details regarding this moth are given by Johnson (1938, 1940) and Hogue et al. (1965).

Comparison of Larvae

The larvae of *walterorum* and *mendocino* are very similar but can be distinguished at all stages of development. Color polymorphism occurs in both species, and the larvae of *mendocino* are especially variable. The first and last instars of *walterorum* have been described (Sala & Hogue, 1958) and all the developmental stages of *mendocino*
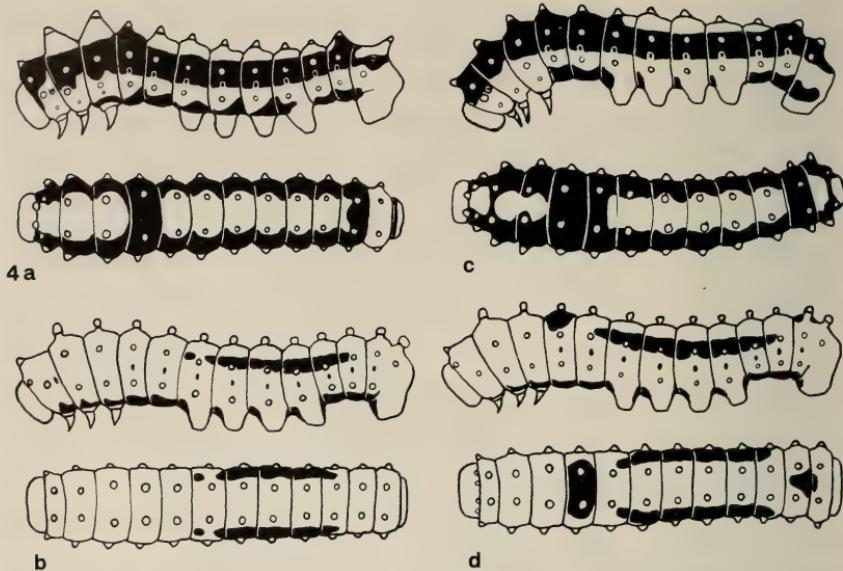
FIG. 4a–d. Dorsal and lateral view of *Saturnia* larvae. Second (4a) and third instar (4b) larvae of *S. walterorum;* second (4c) and third instar (4d) larvae of *S. mendocino.*

were described by Comstock (1960), although he did not recognize the fourth instar as the final larval stage due to the loss of the brood. We provide here a more complete description of variation, and list diagnostic characters for both species.

Figure 4 illustrates the dorsal and lateral view of the second and third instar larvae of *walterorum* and *mendocino.* The setae were omitted to emphasize pattern differences. In second instar *walterorum,* the dorsal scoli of abdominal segments I and VIII are enclosed in posterior and anterior dorsal black bands, while in *mendocino* these two dorsal bands enclose the dorsal scoli of the meso- and metathoracic segments as well as those of abdominal segments I, II, VIII and IX. The meso- and metathoracic dorsal scoli of *mendocino* are also smaller than those of *walterorum.*

In the third instar, *walterorum* lacks the posterior and anterior dorsal bands of abdominal segments I and VIII, which are present in *mendocino.* The length of the lateral stripe is variable in *mendocino,* and may be as illustrated, or may connect with the thoracic transverse band; in extreme cases a connection also exists with the caudal band, forming a rectangle, enclosing the dorsal abdominal scoli. Upon molting into the third instar, the ground color of *mendocino* is yellowish pink dorsally and dull, salmon pink laterally. The day after ecdysis a

rapid color change occurs; some larvae become lemon yellow, others turn light green, while a smaller number are a salmon pink with a yellow tinge. The green phase of both species is probably the most common. A similar polymorphism occurs in *walterorum* except that the yellow phase usually has an orange tint.

The mature larvae of *walterorum* and *mendocino* are very similar and can be reliably separated only by the greater number of dark proleg setae in *mendocino* (Tuskes, 1976). Ferguson (1972) noted that the description by Sala & Hogue (1958) of the mature *walterorum* larvae made no mention of a prominent yellow lateral line seen in *mendocino* and inferred that this was a means to distinguish the two species. This line does exist in *walterorum*, and extends from the caudal area to the metathoracic segment, passing just below the spiracles. Donahue (1979) illustrated in color a mature *walterorum* larva photographed by one of the authors. We have also found that unlike *mendocino* larvae, which pass through only four instars, approximately 62 percent of the *walterorum* have five instars, the remainder matured in four. Furthermore, about 80 percent of the larvae with five instars developed into females. Fourth and fifth instar larvae are identical in color and pattern and as in the third instar, the green color phase is the most common. In *mendocino*, lemon yellow larvae often have a greenish tint, while *walterorum* larvae in this phase are yellowish-orange. The third color form is more difficult to describe but has been called mauve by Comstock (1960) and salmon by Sala & Hogue (1958). We have noted Yolo Co. *mendocino* in this phase are a salmon-pink with a yellowish cast. Infrequently a variation occurs which is a richer color, close to a reddish-brown. Williams (1905) recorded the green form and this brownish phase of *mendocino* from Mt. Shasta, and Tilden (1945) collected this color form in Santa Cruz Co. Interestingly, the color of the third instar larva cannot be used to predict the color phase of the mature larva.

Hybridization Studies

We have directed the results of our hybridization studies toward three areas of investigation: a functional measure of genetic incompatibility between *walterorum* and *mendocino* through all stages of development; an evaluation of potential barriers to interspecific mating; and a comparison of hybrid phenotypes to specimens from geographically intermediate populations.

The results indicate a certain degree of genetic compatibility between *walterorum* and *mendocino*. The successful production of F_1 adults, using either species as the female parent, indicates that the mode of gene expression throughout development is compatible in

the two species, and indirectly implies a great deal of allelic homology. By contrast, developmental incompatibility has been demonstrated in hybrids of closely related species of *Callosamia* (Peigler, 1977) and *Phyciodes* (Oliver, 1978). During the formation of gametes in the F_1 progeny, the once equal representation of chromosomes from each parental species is randomly assorted in meiosis. Dissimilarities in chromosomes can cause aborted gonad or gamete formation especially in the heterogametic sex (Dobzhansky, 1970). Thus, sterile hybrid females are common in studies with *Hyalophora* (Sweadner, 1937; Collins, 1973), and European *Saturnia* (Standfuss, 1900, 1901a, b). Yet in this study fertile F_1 hybrid females were produced when the female parent was *walterorum,* while the reciprocal cross produced sterile females which possessed about half of the normal number of ova. These results suggest that perhaps the observed nonreciprocal sterility is somehow linked to the genetic basis of sexual dimorphism, which is strongly expressed in *walterorum* but less so in *mendocino.* In Lepidoptera ZW represents the heterogametic female sex chromosome combination, and ZZ denotes the male sex chromosomes. Perhaps the action in hybrid females of the Z chromosome from *walterorum* is incompatible with that part of the W chromosome from *mendocino* which affects gametogenesis. In male hybrids of various combinations the eyespot size is close to *walterorum,* while in female hybrids the eyespots grade from small to large, depending on the parentage of the cross (Table 1, Fig. 1). This is additional circumstantial evidence of disruptive effects caused by the Z chromosome of *walterorum.* Further, it appears that at least some of the sexual dimorphism observed in female *walterorum* (ground color and submarginal forewing band) is sex limited and is not carried by alleles on the W chromosome. Though none of these characters are expressed by male *walterorum,* they are transmitted by the male to the F_1 female progeny when mated to a female *mendocino.* In addition, it would also appear that discal eyespot size and ground color are polygenic and not expressed as simple dominant or recessive traits.

Although F_{1a} females were sterile, F_{1b} females backcrossed to the parent species had nearly normal fertility and fecundity. In backcrosses, partial genome integrity is preserved via the non-hybrid parent. By contrast, F_2 females were sterile. High mortality in the F_2 generation may be ascribed to hybrid breakdown, the disruption of highly integrated parts of the genome (Dobzhansky, 1970, 1977).

Analysis of Intermediate Populations

Populations of *Saturnia* exhibiting intermediate characters were found in the central Coast Range (Fig. 3). Three male *Saturnia* were

trapped, using an F_1 female as bait, near Cone Peak, Santa Lucia Mountains, Monterey Co. These specimens are the size of *mendocino* but possess 26 percent larger hindwing eyespots (Fig. 2g). The ventral apical mark appears as a trace, similar to many F_1 male specimens. Ferguson (1972) and Tuskes (1974) cite Tilden's capture of three male *walterorum* in the La Panza Range, San Luis Obispo Co. but upon examining these specimens we found that they are not typical *walterorum*. We collected three additional males which were attracted to a female *mendocino* near La Panza Summit. The La Panza males have larger eyespots than the Cone Peak specimens and exhibit the white apical mark of *walterorum*. They resemble *mendocino* in size and in having a larger hindwing eyespot than forewing eyespot, as do the Cone Peak males (Fig. 2). If the eyespot size relative to forewing length of these intermediate specimens is compared to the Santa Barbara *walterorum*, we find that the hindwing eyespot of the Cone Peak males, and fore- and hindwing eyespots of La Panza males are proportionately larger. As mentioned in Results, difference in overall size accounts for only 10 percent of the difference in eyespot size between typical *mendocino* and *walterorum*. Thus, both the Cone Peak and La Panza *Saturnia* appear like *mendocino* in overall size and in having an eyespot ratio less than one, but have prominent apical marks and larger eyespots; the *walterorum* characters are more pronounced in the more southern La Panza population.

One of the La Panza males was mated to the female *mendocino* and the resulting larvae exhibited mixed larval phenotypes. Five females and one male were reared to maturity; the females were the size of *mendocino* and lacked any trace of a submarginal black forewing band, but showed the ground color of *walterorum*, much like the laboratory F_1 hybrids.

We can offer only tentative conclusions about the taxonomic status of the *Saturnia* in the Santa Lucia and La Panza mountains. A larger sample needs to be collected, especially of the more diagnostic females. However, the available phenotypic evidence, combined with the demonstrated lack of reproductive barriers, and high degree of genetic compatibility in hybrids, suggests that at some time in the past the *Saturnia* in the central California Coast Range could have undergone a period of hybridization and introgression between *mendocino*-like and *walterorum*-like populations. We theorize below that this event may have been secondary to the divergence of these taxa, perhaps during the post Pleistocene xerothermic event.

In summary, *Saturnia mendocino* and *S. walterorum* can best be classified as semispecies, as exemplified by *Drosophila paulistorum*

(Dobzhansky et al., 1977). Morphological differences between the two taxa are slight; mature larvae, cocoons, pupae, and adult males are very similar, while immature larvae and adult females are distinct. No prezygotic barriers to reproduction exist under laboratory conditions. Postzygotic mechanisms act to reduce reproductive fitness in certain primary crosses, but backcrosses can be fertile in both sexes. The F_2 adults are sterile and frequently malformed. The historic isolation between *mendocino* and *walterorum* in the southern Coast Range has probably been topographic. Between the southern Sierra Nevada and the Coast Range there are expanses of desert and numerous small mountain ranges which lack host plants of either species. In the central Coast Range, *Arctostaphylos* chaparral is discontinuous, separated by other types of vegetation and intervening lowlands (Hanes, 1977). Such discontinuities appear to exist in northern Santa Barbara and southern San Luis Obispo counties, and may represent the boundary between the two species.

Phylogeny of *Saturnia* and *Agapema*

Recent phylogenies of Lepidoptera have combined morphological and biogeographical data with a comparative knowledge of foodplant preferences (Ehrlich and Raven, 1965), based on the general finding that host plant choices are taxonomically specific and evolutionarily conservative. Conversely, evolutionary radiation is often accompanied by new host plant associations. Such insect-plant relationships are thought to represent coevolution at the community level (Whittaker & Feeny, 1971; Feeny, 1973).

The American *Saturnia* and the closely related genus *Agapema* seem to represent examples of organisms coevolving with the sclerophyllous members of the Madro-Tertiary flora in western North America. While fossils of these moths are lacking, fossil records of their present day host plants do exist, and knowledge of floral distribution through time provides a framework for a phylogenetic discussion. We must assume that the present day host plants of *Saturnia* and *Agapema* reflect ancient associations, at least at the family level. Before reviewing the fossil flora evidence, we discuss our reasons for including *Agapema* in the discussion and briefly compare the host plants of Eurasian *Saturnia* and their allies with their North American relatives.

The genus *Agapema* is morphologically distinct from *Saturnia* but is closely related to it; Ferguson (1972) separates these genera but Michener (1952) treated *Agapema* as a subgenus of *Saturnia*. Many European and Asian *Saturnia*, as well as related genera such as *Dictyoploca* and *Caligula* are similar to *Agapema* in pattern and color-

ation and are also sexually monomorphic nocturnal fliers. The larvae of *Dictyoploca* and *Caligula* are adorned with long hairs and bear a resemblance to the larvae of *Agapema* in this respect. As noted by Hogue et al. (1965) the nocturnal female of *S. albofasciata* somewhat resembles the nocturnal gray-colored adults of *Agapema*. *Saturnia albofasciata* also resembles the European *S. pavonia* in flight rhythm and sexual dimorphism, and an ancestral link between these two species has been suggested by Hogue et al. (1965). Yet, Ferguson (1972) notes the genitalia of *Agapema* are more primitive and quite similar to *S. pavonia*, while the three American *Saturnia*, especially *albofasciata*, are more specialized and divergent from the European *Saturnia*. Lemaire (1979) also stresses the uniqueness of the American *Saturnia* (which he places in the subgenus *Calosaturnia*) and within this group he further recognizes *S. albofasciata* as the most divergent member, even though this species resembles Old World species in retaining the aedeagus, which is lost in *S. walterorum* and *S. mendocino*. Thus the similarities between *S. pavonia* and *S. albofasciata* may be parallelisms; such phenotypic and phenological flexibility is characteristic of Saturniidae in general.

The Old World *Saturnia*, as well as the related Eurasian genera *Caligula*, *Cricula*, and *Dictyoploca*, tend to be polyphagous; important host plant families include Ericaceae, Rosaceae, Salicaceae, and Fagaceae, but not, apparently, Rhamnaceae. Several trends are apparent in comparisons of New and Old World host plants. The ericaceous preference of *S. pavonia* is seen in *S. walterorum* and *S. mendocino*, but not in the superficially similar *S. albofasciata*, thus further substantiating a more derived rather than ancestral status for this species. *Saturnia albofasciata* does retain a widespread Old World preference for rosaceous plants in its inclusion of *Cercocarpus* as a host plant, although it is possible this plant merely resembles Rhamnaceae biochemically and that this is the basis for its utilization by the moth. Rhamnaceae may be a new host plant group acquired during the New World evolution of *Saturnia* and *Agapema*. The larvae of *A. homogena* feed on *Rhamnus* in Arizona (Mr. Kenneth Hansen, pers. comm.) and are said to refuse *Arctostaphylos* in captivity. Other species of *Agapema* feed principally on *Condalia* and related Rhamnaceae. As mentioned above, *S. albofasciata* feeds on *Ceanothus* (Rhamnaceae). Thus, morphological similarity establishes a tie between *Agapema* and Eurasian *Saturnia* and related genera, and general morphology and host plant selection provides a link between *Agapema* and American *Saturnia*, especially *albofasciata*. *Rhus laurina* and *R. integrifolia* are food plants only of *walterorum* and may be associated with this species' divergence from *mendocino*, as dis-

TABLE 3. Fossil records of present day *Saturnia-Agapema* host plant genera.

MIOCENE	PLIOCENE
Techachapi; Southern Calif. (Axelrod, 1939):	Anaverde, Mt. Eden, Piru George; Southern Calif. (Axelrod, 1950):
Arctostaphylos glandulosa *Cercocarpus betuloides* *Rhamnus californica* *Rhus integrifolia* *Ceanothus cuneatus*	*Arctostaphylos* *Cercocarpus* *Rhamnus* *Rhus laurina*
Aldrich-Fallon-Middlegate; Interior Nevada (Axelrod, 1956):	Table Mountain, Remington Hills, Chalk Hills; Cent. Calif. (Chaney, 1944):
Arbutus *Ceanothus* *Cercocarpus*	*Arbutus* *Ceanothus cuneatus* *Cercocarpus* *Arctostaphylos* *Rhamnus*
Mint Canyon; Southern Calif. (Axelrod, 1940):	Mulholland; Coastal Central Calif. (Axelrod, 1944):
Ceanothus cuneatus *Cercocarpus betuloides* *Rhamnus crocea*	*Ceanothus* *Cercocarpus* *Rhamnus* *Arbutus* *Rhus laurina*

cussed below. In summary, no American species in either genus possesses both primitive Old World genitalic structure and host plant preferences. It is our thesis that these New World genera became specialized by coevolving with their host plants as climate and topography changed during the late Tertiary and Quaternary.

The evolution of sclerophyllous plants, as part of the Madro-Tertiary flora, with which the *Saturnia* are closely associated, has been dealt with in detail by Axelrod and others (Table 3). Axelrod (1977) presents a summary discussion and we cite other original papers. His thesis rests on the premise that ancient climates can be deduced from the species composition of geofloras, whose leaf shapes and structures are clues to their ecological requirements. In many cases these ancient species closely resemble living forms. As climates and topography changed, the distribution of plant species shifted accordingly. Those groups preadapted to xeric conditions underwent rapid speciation (e.g., *Ceanothus*, *Arctostaphylos*, *Quercus*), while plants dependent on summer rain were displaced as the climate became cooler and drier. Thus, during the Miocene-Pliocene there was a general coastward movement of Madro-Tertiary flora.

The Madro-Tertiary flora in the early Tertiary developed as more

xeric tolerant elements of a very generalized, diverse woodland, including deciduous species, which enjoyed a moderate climate of summer rains and mild winters. Due to the lack of major topographic relief and the widespread floras, it is possible that in the Miocene the *Saturnia-Agapema* ancestral stock existed as one or a few distinct species, having arrived from Asia via a land bridge during Eocene-Oligocene times. Yet, modern host plant relationships could have evolved at this time.

At the time of the Pliocene the various genera of food plants utilized by *Saturnia* and *Agapema* were all members of a single community which extended as a more or less continuous flora throughout the present day Great Basin and Southwest. Border redwood, redwood, and chaparral communities occurred to the north in the Sierra, then only 1000–1300 m in elevation. The middle Pliocene was probably the last period when central and southern California coastal floras were intermixed (Chaney, 1944). We can surmise that *Saturnia* had not necessarily diverged into the precursor populations of *mendocino* and *walterorum* since the distribution of *Arctostaphylos* was so widespread. Perhaps the more northern populations also fed on *Arbutus* as members of a tan oak-madrone-canyon oak community, while southern populations extended their ecological tolerance into a warmer coastal community containing *Rhus*.

Climatic and geological factors in the late Pliocene and Pleistocene caused segregation of separate plant communities from more generalized communities. More extreme seasonal fluctuations developed and in general the climate was becoming cooler and drier. The continuing rise of the Sierra Nevada and the subsequent uplift of the Santa Ana and San Gabriel Mountains as well as the Coast Ranges occurred at this time. These altitudinal changes and the accompanying rain shadows produced dramatic environmental clines. Chaparral as a distinct and widespread community type probably first appeared in the Pleistocene as an altitudinal segregate on the lower slopes of uplifting mountains. The final disappearance of summer rains gave rise to a Mediterranean climate along the coast but the interior penetration of the moderating coastal climate was eliminated as mountain building occurred. We can hypothesize that as the southern California *Rhus-Arctostaphylos* association began to separate into montane and coastal communities the moths expanded their distribution accordingly. Northern California populations diverged into *mendocino* on manzanita in the Coast Range and in the Sierras, separated by an increasingly inhospitable valley. A northern bridge of *Arctostaphylos* and perhaps *Arbutus* in the Sierra-Cascades provided genetic continuity to this wide ranging species.

Saturnia albofasciata probably arose as a separate entity in southern California in association with the more xeric-adapted *Ceanothus cuneatus* and *Cercocarpus betuloides.* Its appearance in the Coast Ranges would then be one of invasion as *C. cuneatus* and *C. betuloides* spread on the uplifting coastal mountains. Thus, the sympatry of *mendocino* and *albofasciata* may be rather recent.

The rain shadow of the Sierras and southern California mountains produced an intervening desert which isolated the Arizona derivatives of *Saturnia. Agapema homogena* may be a relict species as it now inhabits montane areas of summer rains (Colorado, Arizona, New Mexico, west Texas and portions of northern Mexico) and emerges in early summer. The desert species of *Agapema* probably appeared at this time although it is possible that they speciated earlier in Mexico and subsequently invaded the developing American deserts to the north.

The phenomenon of the xerothermic period may explain the apparently intermediate populations of *Saturnia* in the Santa Lucia and La Panza mountains. The xerothermic of 3000 to 8500 years ago was a sudden warming period between the last glaciation and the more recent cooling period (Axelrod, 1966). This change in climate appears to have forced chaparral species such as *Arctostaphylos glauca* Lindl. north into the Coast Ranges such that relict populations now exist as far north as Mt. Hamilton. Similarly, *Rhus laurina* and *R. integrifolia* have an oddly disjunct population near Cayucos, 130 km N of their normal range. The northern movement of all these plants during a brief period of warmth may have produced a temporary event of hybridization and introgression between *S. mendocino* and *S. walterorum.*

We can hypothesize that the *Saturnia* responded to the same environmental changes as their host plants and evolved phenological and developmental adaptations. The highly synchronized spring adult emergence and facultative egg development of *mendocino* and *walterorum* allow the larvae to exploit the early growth of their food plants. The egg of *albofasciata* represents an alternative modification, allowing the larva to overwinter and emerge in the early spring to feed on new growth. Perhaps the fall flight of this species is a direct result of this adaptation. The genetic potential for this adaptation may well be ancestral; an overwintering egg occurs in the Asian *Caligula* and *Dictyoploca,* and in Arizona populations of *Agapema galbina.* The pupae of *walterorum* and *mendocino* pass through the hot dry summer months, as well as the winter. The open mesh cocoon construction is especially well developed in the desert species of *Agapema,* and much less so in the montane *A. homogena.* The loose mesh cocoon may aid in ventilation, keeping the pupa cooler.

Hogue et al. (1965) proposed that both *mendocino-walterorum* and the genus *Agapema* arose sympatrically from an *albofasciata*-like ancestor by means of dual mutations affecting coloration and flight times, such that dull colored night flying mutant males would encounter more similarly colored nocturnal females, and brightly colored mutant diurnal females would encounter normal brightly colored diurnal males. In this way arose the brightly colored diurnal *walterorum-mendocino* line, which resembles male *albofasciata*, and the dull colored nocturnal *Agapema*, which are similar to the female of *albofasciata*. It should be pointed out that female flight occurs only after mating, and that pheromones, not chance encounters in flight, control mating response. Furthermore, Saturniidae are poor candidates for sympatric speciation as judged by the criteria of current models (Wilson et al., 1975). They are present in large mobile, more or less randomly mating populations, in which the uniting of rare mutants is unlikely. Since the pheromone system controls mating, mutants with allochronic mating behavior would be severely selected against. Rather, we feel that the *Saturnia-Agapema* phylogeny is one of coevolution with Madro-Tertiary flora in which moths and their sclerophyllous host plants adapted to changing climate, primarily by altering developmental phenomena. The continual lateral and altitudinal redistribution of plant communities, especially during the Pliocene-Pleistocene, provided ample opportunity for allopatric speciation to occur. In this context the West Coast *Saturnia* are important examples of endemic species which evolved in response to the appearance of a Mediterranean climate.

LITERATURE CITED

AXELROD, D. I. 1939. A Miocene flora from the western border of the Mohave desert. Carnegie Inst. Wash. Pub. 516: 1–128.
———— 1940. The Mint Canyon flora of southern California: a preliminary statement. Amer. J. Sci. 238: 577–585.
———— 1944. The Mulholland flora. Carnegie Inst. Wash. Pub. 533: 103–146.
———— 1950. The Anaverde flora of southern California. Carnegie Inst. Wash. Pub. 590: 119–158.
———— 1956. Mio-Pliocene floras from west-central Nevada. Univ. Calif. Pub. Geol. Sci. 33: 1–316.
———— 1966. The early Pleistocene Soboba flora of Southern California. Univ. Calif. Pubs. Geol. Sci., 60: 1–109.

——— 1977. In Barbour, M., & J. Major, eds., Terrestrial vegetation of California. Wiley, New York. 1002 pp.

BAKKER, E. 1971. An island called California. Univ. Calif. Press, Berkeley. 357 pp.

BEHRENS, J. 1876. Description of a new saturnian. Can. Entomol. 8: 149.

CHANEY, R. 1944. Pliocene floras of California and Oregon. Carnegie Inst. Wash. Pub. 553: 1–407.

COMSTOCK, J. A. 1960. Life history notes on a saturniid and two lasiocampid moths from California. Bull. So. Calif. Acad. Sci. 59: 170–175.

COLLINS, M. M. 1973. Notes on the taxonomic status of *Hyalophora columbia* (Saturniidae). J. Lepid. Soc. 27: 225–235.

DOBZHANSKY, T. 1970. Genetics of the evolutionary process. Columbia Univ. Press, New York. 505 pp.

DOBZHANSKY, T., F. AYALA, G. L. STEBBINS & J. W. VALENTINE. 1977. Evolution. Freeman, San Francisco. 572 pp.

DONAHUE, J. P. 1979. Strategies for survival, the cause of a caterpillar. Terra 17: 3–9.

EHRLICH, P. R. & P. RAVEN. 1965. Butterflies and plants: a study in coevolution. Evolution 18: 586–608.

FEENY, P. 1973. In Gilbert, L. & R. Raven, eds., Coevolution of animals and plants. Symp. 1st Intern. Congr. Syst. Evol. Biol. Univ. Texas Press, Austin.

FERGUSON, D. C. 1972. The moths of America north of Mexico. Fasc.20.2A, Bombycoidea (in part) Classey, London. pp. 155–269, pls. 12–22.

HANES, C. L. 1977. In Barbour, M., & J. Major, eds., Terrestrial vegetation of California. Wiley, New York. 1002 pp.

HOGUE, C. L., F. P. SALA, N. MCFARLAND & C. HENNE. 1965. Systematics and life history of *Saturnia (Calosaturnia) albofasciata* in California (Saturniidae). J. Res. Lepid. 4: 173–184.

JOHNSON, J. W. 1938. *Calosaturnia albofasciata* species nova (Lepidoptera, Saturniidae). Bull. Brooklyn Entomol. Soc. 33: 128–130.

——— 1940. The allotype of *Calosaturnia albofasciata* (Lepidoptera, Saturniidae). Bull. Brooklyn Entomol. Soc. 35: 46–50.

LEMAIRE, C. 1978. Les Attacidae Americains. Edition C. Lemaire. 238 pp.

MAJOR, J. 1977. In Barbour, M., & J. Major, eds., Terrestrial vegetation of California. Wiley, New York. 1002 pp.

MICHENER, C. D. 1952. The Saturniidae (Lepidoptera) of the Western Hemisphere. Bull. Amer. Mus. Nat. Hist. 98: 339–501.

MIYATA, T. 1974. Studies on diapause in *Actias* moths (Lepidoptera, Saturniidae) I. Photoperiodic induction and termination. Kontyu 42: 51–63.

OLIVER, C. G. 1978. Experimental hybridization between the nymphalid butterflies *Phyciodes tharos* and *P. campestris montana*. Evolution 32: 594–601.

PEIGLER, R. S. 1977. Hybridization of *Callosamia* (Saturniidae). J. Lepid. Soc. 31: 23–34.

SALA, F. P. & C. L. HOGUE. 1958. Descriptions of the early stages and male imago and notes on the life history of *Saturnia walterorum* (Saturniidae). Lepid. News 12: 17–25.

STANDFUSS, M. 1900. Synopsis of experiments in hybridization and temperature made with Lepidoptera up to the end of 1898. Entomologist 33: 340–348.

——— 1901a. Ibid. 34: 11–13.

——— 1901b. Ibid. 34: 75–84.

SWEADNER, W. R. 1937. Hybridization and the phylogeny of the genus *Platysamia*. Ann. Carnegie Mus. 25: 163–242.

TILDEN, J. W. 1945. Notes on some moths of the family Saturniidae (Lepidoptera). Pan Pacific Entomol. 21: 32–33.

TUSKES, P. M. 1974. The distribution and larval foodplant relationships of *Saturnia walterorum* (Saturniidae). J. Lepid. Soc. 28: 172–174.

——— 1976. A key to the last instar larvae of West Coast Saturniidae. J. Lepid. Soc. 30: 272–276.

WHITTAKER, R. & P. FEENY. 1971. Allelochemics: chemical interactions between species. Science 171: 757–770.

WILLIAMS, C. M. & P. L. ADKISSON. 1964. Physiology of insect diapause. XIV. An endocrine mechanism for the photoperiodic control of pupal diapause in the oak silkworm, *Antheraea peryni*. Biol. Bull. 127: 511–525.

WILLIAMS, F. X. 1905. Notes on the larvae of certain Lepidoptera. Entomol. News. p. 153.

WILSON, A. C., G. L. BUSH, S. M. CASE & M. C. KING. 1975. Social structure of mammal populations and rate of chromosomal evolution. Proc. Natl. Acad. Sci. (U.S.A.) 72: 5061–5065.

RECENT ADDITIONS TO THE COLLECTION OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Dr. Cyril F. dos Passos has donated his collection of 65,382 butterflies to the American Museum of Natural History. Of this total, 64,052 specimens are mounted and identified; 57,870 are from North America and 6182 are from Europe; 1330 are unmounted or unidentified. Included in the collection are 464 paratypes (no holotypes or allotypes) and 617 slides (124 venation, 493 genitalia). Dr. dos Passos started building his collection in 1929; it undoubtedly represents the single largest and most complete one of North American butterflies ever made by one individual. It far surpasses the two previous large collections of butterflies (no moths) received by the Department of Entomology, namely those of J. D. Gunder (27,000 North American specimens, received in 1937) and V. G. L. van Someren (23,000 African specimens, received in 1970). The addition of this collection gives the American Museum of Natural History an unrivaled collection of North American butterflies.

The museum has also received the collection of the late Bernard Heineman, consisting of 7075 mounted butterflies and moths. Of these, 2857 were from Jamaica, with the great majority being butterflies. This is the largest private collection of Jamaican butterflies ever made, and it served as the starting point for the 1972 book entitled, "Jamaica and its butterflies" by F. Martin Brown and Bernard Heineman. The other 4218 specimens represent a world-wide collection made by Mr. and Mrs. Heineman on their various trips throughout the world.

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OCCURRENCE AND SIGNIFICANCE OF AN UNUSUAL PHENOTYPE OF *COLIAS CESONIA* STOLL (PIERIDAE) IN THE UNITED STATES

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ABSTRACT. The unusual female form of *Colias cesonia* Stoll called immaculsecunda has been recorded from several localities in the southern United States. This form is thought to be a migrant from some Mexican *cesonia* populations and not a genetic aberration appearing sporadically in separate U.S. populations.

Colias (Zerene) cesonia cesonia Stoll is a familiar butterfly throughout much of the southern United States. The male possesses a prominent "dog-face" on the DFW while the female exhibits a less distinct but still recognizable "dog-face." A Neotropical subspecies, *C. c. therapis* (F. & F.), possesses no remnants of such a mark. A related species, *Colias (Zerene) eurydice* Bdv., occurs in California and Mexico. Males of *eurydice* also possess a distinct "dog-face" but females of this species have no "dog-face" and possess only rudimentary dark markings. There is a ♀ form of *cesonia*, however, which also lacks the "dog-face." This paper surveys the occurrence of this form in the United States and Mexico (as known) and discusses possible origins of this form.

Colias (Zerene) cesonia cesonia Stoll ♀ form immaculsecunda Gunder was first described from two specimens, one from Arizona (23 September 1927) and one from Missouri (27 September 1917) (see Gunder, 1928). The original description is as follows: "Primaries: with greatly reduced black markings; outline of 'dog-face' not clear cut, having outline at 'forehead' incomplete. Secondaries: immaculate of all usual marginal designs, cell blotch remaining as usual. Wings beneath as in typical *cesonia*, yet not over ruddy." Gunder (1928) illustrates both the holotype (from Arizona) and paratype (from Missouri) and classifies this taxon as a "form ♀," which simply indicates "forms belonging to only one sex" (Gunder, 1927).

Subsequently, this form has been reported from other localities. From Arizona, Brown (1965) reported three specimens each in different years (1950, 1957, 1963) but all in September. The 1963 specimen is illustrated (Brown, 1965: fig. 3) as an unnamed aberration. Stallings (1941) reported three specimens from Sumner Co., Kansas, on 15 April 1938. Bennett (1968) reported one specimen each in October and November of 1966 in Lubbock, Lubbock Co., Texas.

In my personal collection is a specimen collected 27 October 1968 at the Brackenridge Field Laboratory in Austin, Travis Co., Texas
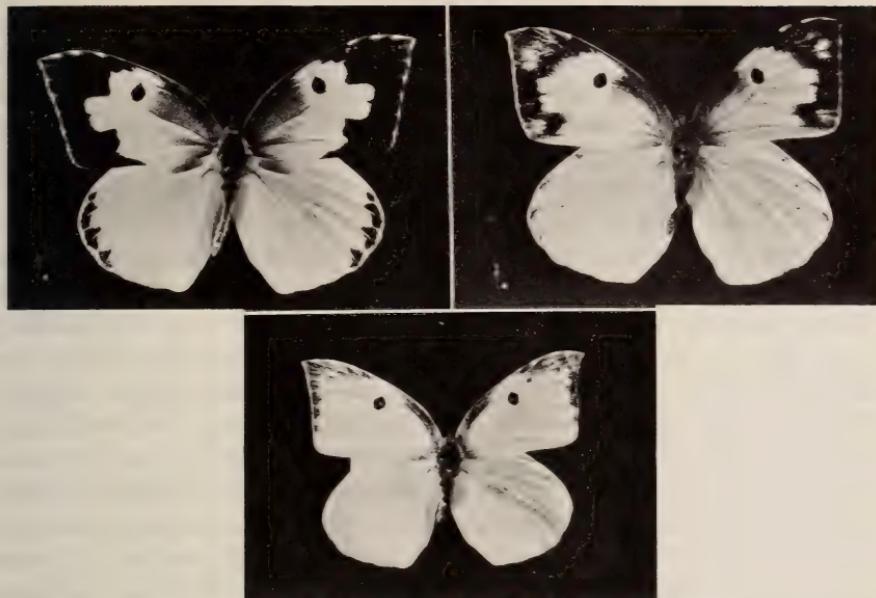
FIG. 1. Forms of *Colias (Zerene) cesonia* from Austin, Travis County, Texas. Clockwise from upper left: normal ♂, 1 November 1968; normal ♀, 19 October 1968; immaculsecunda, ♀ form, 27 October 1968.

(Fig. 1). Other specimens were seen at this time. Additionally, my field notes record the occurrence of immaculsecunda in Austin in late November 1971, although no specimens were taken. C. J. Durden (pers. comm.) also observed this form in the Austin area in late summer and fall 1971.

The specimen in my collection is slightly smaller than normal females collected at the same time (wingspan—53 mm vs. normal 60 mm). This unusual phenotype exhibits the same degree of pink suffusion of the VFW and VHW as do the normal specimens collected at the same time. This suffusion has been called rosa McNeill by some but is merely a seasonal influence which occurs in other subspecies of *cesonia* as well. The rosa influence of the 27 October 1968 Austin specimen is slightly less than one specimen figured in Howe (1975: plate 75, fig. 9). Masters (1969) demonstrates the occurrence of this roseate form in *Colias cesonia therapis* (F. & F.) with the dry season in Venezuela. The similarity in the rosa influence in both normal and immaculsecunda forms indicates that separate, and probably unlinked, genetic systems are involved. The 1968 Austin specimen of immaculsecunda exhibits slightly greater reduction of black margins of the DFW than shown by Bennett (1968); the specimen looks

very much like the Venezuelan subspecies *therapis* (see Masters, 1969) except that immaculsecunda retains the discal spot of the DFW (the "eye" of the dog-face). *Colias (Zerene) eurydice* Bdv. ab. nigrocapitata Riddell is somewhat similar to immaculsecunda in that it retains dark margins along the DFW apex but also retains the DFW discal spot (Riddell, 1941).

This ♀ form immaculsecunda has also been reported from Mexico. Vasquez G. (1952) reviewed all forms of *C. cesonia* known from Mexico. She could find no true immaculsecunda but reported "*forma feminina* n, *parecida a* immaculsecunda" which is very close to Gunder's (1928) figures but has slightly more reduced melanic markings. Locality records were from the state of Hidalgo as well as the Distrito Federal in the high-elevation central part of Mexico. No collection dates are given. L. E. Gilbert has a specimen in his collection dated 16 January 1969 from near Naranjo, San Luis Potosi. Hoffmann (1940) simply lists immaculsecunda from Mexico without reporting collection localities; he reports *cesonia* as occurring "*en todo el pais.*" However, Brown (1944) did not find this form in several collections from northern and central Mexico.

Times of occurrence of immaculsecunda in Texas reveal a significant pattern. The years 1966, 1968 and 1971 were all seasons of unusual abundance or occurrence of Lepidoptera involving population movements of various species northward from Mexico. Breeding of two heliconians [*Heliconius charitonius vasquezae* (Comstock and Brown) and *Dryas julia moderata* Stichel] which periodically occur in central Texas during autumn was observed in 1966 (Rickard, 1967, 1968). During 1968 these two heliconians were abundant in the Austin area as early as June 1968 (Neck, 1978). Two factors could explain why immaculsecunda did not appear until October in 1968. Immigration into the area could have occurred only in the fall months. On the other hand, immigration could have occurred earlier in the late spring months but this form was undiscovered by lepidopterists until the fall generation appeared. Two generations, one spring and one fall, are typical of *cesonia* in central Texas. Specimens collected in October 1968 were not worn to a degree that long-distance dispersal by those specimens was indicated. Late summer and autumn 1971 were extremely unusual times for Lepidoptera. A severe drought was broken in late July and early August. Massive northward movements of numerous butterfly species resulted, including one of the rare massive cloud migrations of *Libytheana bachmanii larvata* (Strecker) (Helfert, 1972; Neck, in prep.). The northward movement of the tropical butterfly *Dione moneta* during unusual climatic conditions was reported and analyzed by Gilbert (1969).

Occurrence of immaculsecunda in Texas during years of unusual northward movements of butterfly populations from Mexico indicates the possibility that this form is a resident female phenotype in some Mexican populations. Of the other reports of immaculsecunda in the United States (see above review) all but one were collected in the period September to November. The sole exception involves the collection of three specimens collected in Kansas in mid-April. April is an early date for *cesonia* to be found in Kansas; *cesonia* is most common in Kansas from August to October (Calkins, 1932; Field, 1928). Field (1928) does report specimens of *cesonia* in mid-May 1935. Weniger (1945) reported specimens in late June 1944.

If one accepts the thesis that immaculsecunda is an immigrant form from Mexico, these April Kansas specimens have one of two origins. They either represent an overwintering brood or an early season migration. Migrations of sub-tropical and tropical butterflies to latitudes as far north as Kansas are common but generally occur in summer and autumn (Calkins, 1936; Howe, 1958). At least one species, *Agraulis vanillae* (L.), makes almost annual migrations to Kansas, where it fails to overwinter (Randolph, 1927). Note should be made of the capture of the tropical species *Adelpha bredowii* (Geyer) by V. F. Calkins in Scott Co., Kansas on 2 May 1936 (Field, 1938). One may assume that either origin mentioned above for the April Kansas immaculsecunda could be valid. Howe (1965) felt that *cesonia* in Kansas might be a breeding migrant, although "strong evidence supports the idea that at least a few adults of *cesonia* hibernate here as well." Overwintering of *cesonia* has been suspected in areas of the neighboring state of Missouri (Masters, 1969), including the actual observation of a hibernating adult in St. Louis Co. (O'Bryne, 1941).

I believe enough evidence (admittedly circumstantial) exists to assume that immaculsecunda Gunder may well be a resident phenotype in some populations of Mexico. I do not believe that it is a genetic aberration which appears independently in various populations as has been assumed by many workers. Collectors in Mexico should make efforts to sample and study populations of *cesonia* in the field to determine the true taxonomic standing of immaculsecunda Gunder. While it has been suggested that immaculsecunda is a form responding to cold weather (Bennett, 1968), cold weather generally results in melanistic forms, not forms lacking normal melanic pigment (Robinson, 1971: 210).

LITERATURE CITED

BENNETT, D. 1968. Two variant females of *Colias* (*Zerene*) *cesonia* (Pieridae). J. Lepid. Soc. 22: 253.

BROWN, F. M. 1944. Notes on Mexican butterflies. II. Pieridae. J. N.Y. Entomol. Soc. 52: 99–119.

BROWN, K. S., JR. 1965. Some comments on Arizona butterflies (Palilionoidea). J. Lepid. Soc. 19: 107–115.

CALKINS, V. F. 1921. The rhopalocerous Lepidoptera of Scott County, Kansas. Entomol. News 43: 210–260.

—— 1936. Some unusual butterfly records taken in Scott County, Kansas. Bull. Brooklyn Entomol. Soc. 31: 66–68.

FIELD, W. D. 1938. A manual of the butterflies and skippers of Kansas (Lepidoptera, Rhopalocera). Bull. U. Kans., Biol. Ser. 39(10): 1–328.

GILBERT, L. E. 1969. On the ecology of natural dispersal: *Dione moneta poeyii* in Texas (Nymphalidae). J. Lepid. Soc. 23: 177–185.

GUNDER, J. D. 1927. Transition forms (Lepid., Rhopalocera). Entomol. News 38: 263–271.

—— 1928. A review of genus *Zerene* Hbn. in the United States (Lepid., Rhopalocera). Pan-Pac. Entomol. 4: 97–102.

HELFERT, M. R. 1972. Migratory behavior of the snout butterfly, *Libytheana bachmanni larvata* (Strecker). Entomol. News 83: 49–52.

HOFFMANN, C. C. 1940. Catalogo sistematico y zoogeografico de los lepidopteros Mexicanos. An. Inst. Biol. Mex. U. Nac. 11: 639–739.

HOWE, W. H. 1958. Capture of a *Eunica tatila* (Nymphalidae) in Kansas. Lepid. News 12–25.

—— 1965. Status of *Agraulis vanillae* in Missouri and Kansas. J. Lepid. Soc. 19: 33–34.

—— 1975. The butterflies of North America. Doubleday & Co., Garden City, N.Y., 633 pp.

MASTERS, J. H. 1969a. Butterflies of Lynch Hollow, Camden County, Missouri. J. Kans. Entomol. Soc. 42: 133–141.

—— 1969b. Seasonal variation of *Colias cesonia therapis* in Venezuela (Pieridae). J. Lepid. Soc. 23: 251–253.

NECK, R. W. 1978. Climatic regimes resulting in unusual occurrences of rhopalocera in central Texas in 1968. J. Lepid. Soc. 32: 111–115.

—— ms. Report and analysis of migrating clouds of the snout butterfly, *Libytheana bachmanni larvata* (Strecker) (Libytheidae).

O'BRYNE, H. I. 1941. The hibernation in Missouri of *Zerene cesonia* (Stall) and *Euptoieta claudia* (Cram. Lepid.: Pieridae and Nymphalidae). Entomol. News 52: 181–183.

RANDOLPH, V. 1927. On the seasonal migrations of *Dione vanillae* in Kansas. Ann. Entomol. Soc. Amer. 20: 242–244.

RICKARD, M. A. 1967. An aberrant *Heliconius charitonius* (Nymphalidae). J. Lepid. Soc. 21: -248.

—— 1968. Life history of *Dryas julia delia* (Heliconiidae). J. Lepid. Soc. 22: 75–76.

RIDDELL, J. 1941. Some remarkable forms and aberrations in the subgenus *Zerene* Hubner (Lepidoptera, Pieridae). Trans. Roy. Entomol. Soc. London 9: 447–457.

ROBINSON, R. 1971. Lepidoptera genetics. Pergamon, Oxford, 687 pp.

STALLINGS, D. B. 1941. Aberrations found in Kansas (Lepidoptera). J. Kans. Entomol. Soc. 14: 72.

VASQUEZ G., L. 1952. Observaciones sobre pieridos Mexicanos con descriptions de algunas formas nuevas. Ant. Inst. Biol. Mex. U. Nac. 23: 257–267.

WENIGER, D. 1945. A list of butterflies (Rhopalocera) collected in Cowley County in 1944. J. Kans. Entomol. Soc. 18: 112–120.

THE LIFE HISTORY AND BEHAVIOR OF *EUPROSERPINUS EUTERPE* (SPHINGIDAE)

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ABSTRACT. *Euproserpinus euterpe* Hy. Edwards is a small day flying sphinx moth which occurs in southern California. Adults are active from late February to early April. The larval host plant is a primrose in the genus *Camissonia*. Females frequently oviposit on an imported plant, *Erodium*. Larvae from eggs deposited on *Erodium* do not survive, and mistakes in oviposition may contribute to the rarity of the moth. Evidence is also presented which suggests that the type locality for this moth is not San Diego County.

Henry Edwards described *Euproserpinus euterpe* in 1888, based on a single male specimen which had been collected in southern California. Until recently, the only other specimens known were a pair in the Clark collection lacking data; but the female had been in a collection since at least 1888 (Clark, 1919). The observation that no additional specimens had been collected, suggested to some that *euterpe* no longer existed in southern California (Comstock, 1938; Hodges, 1971). Then in 1974, Mr. Chris Henne rediscovered *euterpe*, and collected the first specimens in nearly 90 years. In this paper we discuss the biology of this unique sphingid, and describe the immature stages for the first time. The genus contains two additional species, *E. wiesti* Sperry, and *E. phaeton* Grote & Robinson. Of the three species, *phaeton* is the most commonly collected species, and was the only member of the genus whose biology was known (Comstock & Dammers, 1935).

Description of Ova and Larvae
Figs. 1–4

Ova. Light green and oblong, measuring 1.0 by 1.1 mm (Fig. 1).
First Instar. (Fig. 2) **Head:** Black; diameter 0.5 mm. Clypeus white. **Body:** Ground color yellowish-green. Length 4.5 mm; width 0.8 mm. True legs black. Prolegs yellow with anterior black patch. Spiracles black. Scoli are microscopic, black and bulb-shaped. Prothoracic shield black. Anal shield black. Anal horn black; length 0.3 mm.
Second instar. Head: Dark brown; diameter 0.8 mm. Clypeus dark brown. **Body:** Ground color green. Ventral surface green. Subspiracular area and lateral surface of prolegs pink. Dorsal and lateral surface green. Body covered with numerous microscopic black setae. Scoli black. Body length 6.7 mm; width 1.4 mm. True legs black. Prolegs pink. Spiracles black. Prothoracic shield black. Dorsal area proximal to anal horn pink. Anal shield black. Anal horn black; length 0.4 mm.
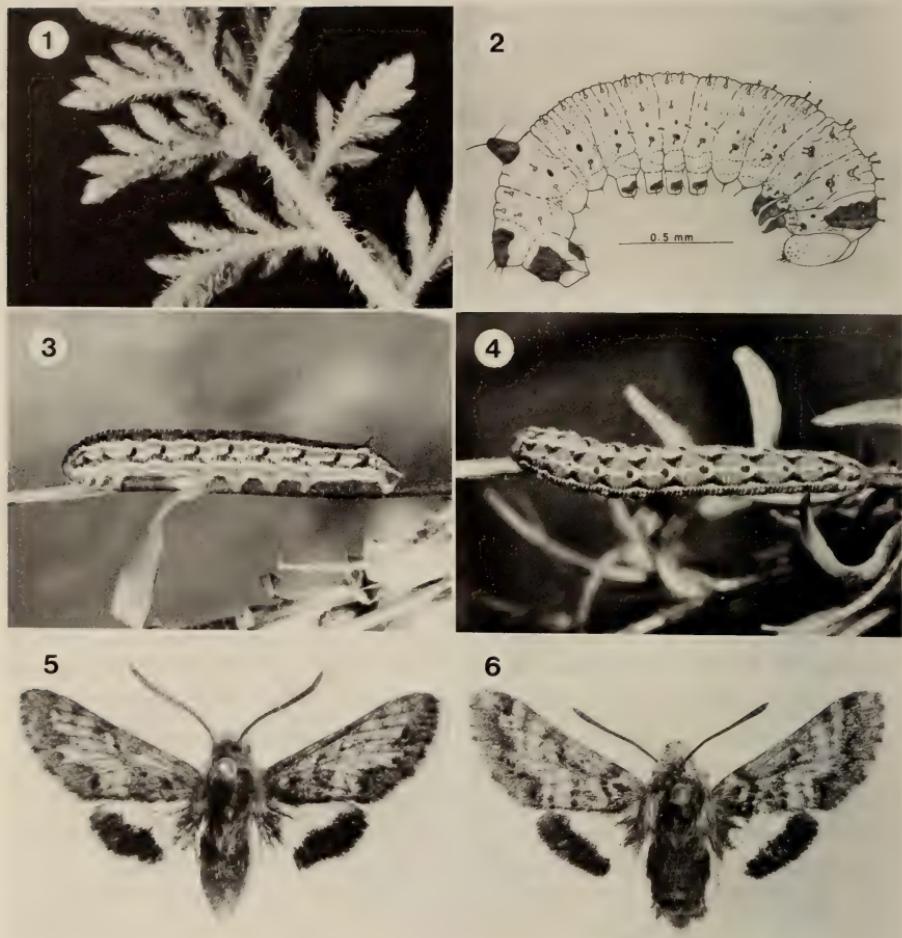
FIGS. 1–6. **1,** Egg of *E. euterpe* on *Erodium;* **2,** First instar larva of *E. euterpe;* **3,** Lateral view of fifth instar larva; **4,** Dorsal view of fifth instar larva; **5,** Male *E. euterpe;* **6,** Female *E. euterpe.*

Third instar. Head: Dark brown; diameter 1.3 mm. Clypeus dark brown. **Body:** Ground color green and red. Ventral surface green. Subspiracular area and lateral surface of prolegs red. Dorsal and lateral surface green. Partially formed dorsal red band extending from base of horn to head on each side of mid-dorsal area. Mid-dorsal area green. Body covered with numerous microscopic bulb-shaped secondary setae. Body length 12.1 mm; width 2.0 mm. True legs black. Prolegs red. Spiracles red. Prothoracic shield brown. Anal shield black. Posterior area from base of horn to anal shield red. Anal horn black; length 0.4 mm.

Fourth instar. Head: Red; diameter 2.1 mm. Clypeus red. **Body:** Ground color green and red. Ventral surface green. Subspiracular area and lateral surface of prolegs red. Subspiracular white line extending from prothoracic segment to anal prolegs. Subdorsal and supraspiracular area light green. Dorsal rust brown lateral band extending from prothoracic segment to base of anal horn. Mid-dorsal area dark green. Black dot

located dorsal to spiracles on abdominal segments I–VIII. Body covered with numerous microscopic bulb-shaped secondary setae now extending from whitish paniculum. Body length 20.0 mm; width 3.4 mm. True legs green. Prolegs red. Spiracles black. Prothoracic shield red. Anal shield red. Posterior area from base of anal horn to anal shield red. Anal horn red; length 0.6 mm.

   Fifth instar. (Figs. 3, 4) **Head:** Dark red; diameter 3.4 mm. Clypeus red. Antenna prominent and cream colored. Adfrontal area light red. **Body:** Ground color green and rust red. Ventral surface grayish-green. Subspiracular area with white line bounded by red on either side and extending length of body. Supraspiracular light green line extending length of body and broken by oblong black spots extending from dorsal edge of spiracles. Pink band dorsal to light green band also extending length of body and partially obstructed by oblong black spots. Subdorsal yellow line extending length of body. Dorsal rust red line extending length of body and interrupted by black V-shaped patch with wide end of patch touching yellow subdorsal line. Mid-dorsal line dark green with black transverse patch on posterior portion of each segment. Body length 32 to 35 mm; width 5 to 6 mm. True legs green. Prolegs red. Spiracles black. Prothoracic shield rust red. Anal shield and horn rust red, length 1.5 mm.

Distribution and Habitat

   Presently, the only known population of *Euproserpinus euterpe* exists in Walker Basin, Kern Co., California. Walker Basin is at an elevation of 1470 m, and is surrounded by mountains well over 2000 m in height. The basin is an agricultural area, primarily consisting of cultivated barley fields, pasture for cattle, and fallow fields. From the time of the rediscovery of *euterpe* in 1974, until the spring of 1979, moths were found in one small section of a fallow barley field. The colony was located in the northwest section of the basin, and encompassed about 4000 m², on sandy soil. The prominent vegetation during the brief flight period includes *Erodium cicutarium* (L.), *Nemophila menziesii* H. & A., *Chrysothamnus*, assorted grasses, and a small composite.

   The plant community surrounding the basin floor is dominated by juniper, oak, sagebrush, or pine, and may limit the distribution of the moth. South of the basin the plant community is oak-grassland, and once over the hills, the elevation drops quickly and conditions become warmer. Near the community of Bodfish, north of Walker Basin, similar habitat was found, but although conditions seemed favorable, no adults were observed.

   In March 1979, many adults were encountered at the original colony site. Tuskes examined other locations in the basin as in previous years, and for the first time observed adults in many new locations. Though adults were widespread in fallow fields and pastures, they were uncommon at all but one location.

Adult Behavior and Flight Period

   Capture records indicate that adults fly from the last week of February to the first week of April, with the peak period during the second

or third week of March. During the flight season, the weather is unpredictable; rain, strong winds, and occasional snow make conditions difficult. Under usual conditions temperatures seldom rise above 18°C, with lows near or below 0°C. Specimens have been observed and captured under stormy conditions when the high temperature for the day was 6°C (J. Johnson, pers. comm.). The early flight of the moths appears to be related to the development of the host plant. Depending upon the season, *Camissonia* seedlings may be found in late February or early March, but by mid-May the majority of the plants are dried and dead.

Adults fly during the warmer parts of the day, usually between 1000 and 1430 h. In the morning, males and females frequently bask on bare patches of soil, dirt roads, or rodent mounds. The majority of the nectaring was observed in the morning at flowers of *Erodium* and *Nemophila*. As the day progresses, males become active fliers, and are difficult to observe or capture. Nectaring or ovipositing adults fly 5–15 cm above the ground. In general, female *euterpe* appear to be slower fliers than female *phaeton*. As the afternoon winds increase, adult basking locations change to areas protected from the wind, such as in washes, behind knolls, or on the ground among bushes. While basking, the ground color of the moths blends well with that of the soil; only their movement as they are about to fly discloses their location. When disturbed, the moths fly about 60 cm above the ground. This flight behavior, combined with their gray coloration, makes them difficult to follow as the moth may easily be confused with its shadow.

Little variation has been observed in adult specimens. In some individuals the submargin of the forewing is about the same color as the rest of the wing, while in others it is the darkest portion of the wing. Some individuals with dark submarginal areas also have a thin gold postmedial band on the forewing (Figs. 5, 6).

Oviposition and Larval Behavior

An unexpected observation was the large number of mistakes made by the females during oviposition. By following ovipositing females and identifying the plants upon which they deposited eggs, we expected to locate *Camissonia*. But time after time females deposited ova on the imported weed, *Erodium cicutarium*. Eggs were laid one, or occasionally two at a time, on the underside of the leaves or on the stems. Larvae reared on *Erodium* did not feed and died of starvation after three days. First instar larvae have been observed to be rather sessile. Considering these observations, the survival of individuals from ova deposited on *Erodium* seems unlikely. Such oviposition errors may contribute to the scarcity of the moth. If this hypothesis is

correct, the probability of successful oviposition may be related to the distribution, abundance, and height of the host plant in relation to *Erodium* during any given spring. *Erodium cicutarium* was introduced to California by the Spanish, and records indicate that it was well established from San Francisco to Baja California by 1775 (Hendry & Bellue, 1936; Robbins, 1940).

A mature larva was collected on *Camissonia*, 6 April 1974 (E. Walter, pers. comm.) and in 1975 Mr. Henne reared *euterpe* larvae on this same species of *Camissonia*. This plant was later identified as *Camissonia contorta epilobiodes* Munz. (by J. McCaskil, Dept. of Botany, Univ. Calif. Davis). We found that larvae of all instars appear to prefer to feed on flowers, and the new apical growth; first instar larvae seemed to feed exclusively on flowers. The disruptive color pattern of fourth and fifth instar larvae allows them to blend well with the colors of the host plant. After feeding, mature larvae rest on the stems near the base of the plant, an area where their pattern blends especially well with that of the plant (Figs. 3, 4). Pupation occurs in the soil, and the pupation chamber is constructed near the surface, perhaps under rocks or other objects. Although larvae in captivity constructed pupal chambers, all perished in the pre-pupal stage.

Pronounced differences were observed in first instar larvae of *euterpe, phaeton,* and *phaeton mojave.* The thoracic shield, anal horn, and patches on the prolegs are heavily sclerotized and dark brown or black in *euterpe* (Fig. 2), but are not sclerotized and green in *phaeton.* First instar setal patterns of *euterpe* and *phaeton* are similar.

Type Locality

In the description of *euterpe*, Edwards (1888) states that the type locality of this moth is near San Diego; however this is almost certainly incorrect. Henry Edwards described many moths and butterflies that he had received from H. K. Morrison, including *euterpe.* Edwards published so many incorrect type localities for the material he had received from Morrison, that Morrison felt compelled to publish a short note in 1883, correcting the errors which Henry Edwards had made. Two of these corrections are of special interest for they are a moth and butterfly from the Kern River, near the present colony of *euterpe.* In addition, the community of Havilah which is located a few miles north of the basin was an active mining town, and served as the county seat until 1874 (Hoover et al., 1966). The same records also indicate access to Havilah and the Kern River was by the wagon road which passed through the Walker Basin. Thus, what is now an out of the way area was once situated along major lines of transportation, and when Morrison traveled to the Kern River to collect *An-*

thocharis morrisonii Hy. Edwards, and *Copaeodes eunus* Hy. Edwards, he would have passed through Walker Basin. Shortly after his publication Morrison died, and thus could not have corrected any later erroneous type localities published by Edwards. Further, scores of *Euproserpinus* from San Diego have been examined but all have been *phaeton*. Comstock (1938), in his effort to locate *euterpe*, suggested that if the type locality was correct, the moth must no longer exist. Based on this information, it is likely that Edwards' type locality for this moth is in fact incorrect, and that the true type locality is in or near Walker Basin.

Because of the small size of the existing colony, *euterpe* was brought to the attention of the Office of Endangered Species and received protection as a threatened species in April of 1980.

Capture Records

1974: 5 ♀♀, CH, Mar. 21; 3 ♀♀, CH, Mar. 22; 2 ♀♀, CL, Mar. 22.

1975: 1 ♂, EW, Feb. 26; 1 ♂, 1 ♀, JJ, Feb. 27; 1 ♂, 1 ♀, JJ, Mar. 29; 2 ♂♂, 1 ♀, EW, Mar. 29; 1 ♀, CH, Mar. 29; 1 ♀, CH, Apr. 2.

1976: 2 ♂♂, MVB, Mar. 17; 1 ♂, 1 ♀, CH, Mar. 17; 1 ♀, CH, Mar. 21.

1977: 1 ♂, CH, Mar. 21; 1 ♀, CH, Apr. 6. 1978: None collected.

1979: 1 ♂, JC, Mar. 18; 1 ♂, 4 ♀♀, PT, Mar. 22; 2 ♂♂, 6 ♀♀, PT, Mar. 23; 1 ♂, 3 ♀♀, PT, Mar. 24; 4 ♂♂, 12 ♀♀, JB, Mar. 24; 1 ♂, 7 ♀♀, JC, Mar. 24; 1 ♂, 5 ♀♀, JC, Mar. 25; 1 ♂, JC, Mar. 29.

Collectors: Chris Henne (CH), Charles Long (CL), Jean Cadiou (JC), Jim Brock (JB), Paul Tuskes (PT), Mike Van Buskirk (MVB), Erich Walter (EW), John Johnson (JJ).

The specimens collected by Henne and Long are deposited in the Los Angeles County Museum of Natural History. Specimens collected by Van Buskirk and the majority of those collected by Tuskes are deposited at the California Academy of Science and the United States National Museum. Preserved larvae have been sent to the Los Angeles County Museum of Natural History.

LITERATURE CITED

COMSTOCK, J. A. 1938. A new race of *Euproserpinus phaeton* from the Mojave Desert. Bull. So. Calif. Acad. Sci. 37: 33–42.

———— & C. M. DAMMERS. 1935. Notes on the early stages of three butterflies and five moths from California. Bull. So. Calif. Acad. Sci. 33: 137–151.

EDWARDS, H. 1888. *Euproserpinus euterpe*, a new species of Sphingidae. Ent. Americana 4: 25–26.

Hendry, G. W. & M. K. Bellue. 1936. An approach to southwestern agricultural history through adobe brick analysis. Univ. New Mexico Bull. 296, pp. 65–72.
Hodges, R. W. 1971. Moths of North America, North of Mexico. Fascicle 21 (Sphingoidae). p. 158, pl. 14.
Hoover, M. D., H. E. Rensch & E. G. Rensch. 1966. Historic Spots in California. Stanford Univ. Press. Stanford, California.
Morrison, H. R. 1883. Localities for diurnals. Papilio 3: 43.
Robbins, R. M. 1940. Alien plants growing without cultivation in California. Univ. Calif. Agr. Expt. Sta. Bull. 637.

BOOK REVIEW

Catalogo dos Ithomiidae Americanos (Lepidoptera) by Romualdo Ferreiera d'Almeida. Conselho Nacional de Desenvolvimento Cientifico e Technologico, Curitiba, Parana, Brazil. 405 pp. 1978. No price stated.

<p align="center">and</p>

Suplemento ao Catalogo dos Ithomiidae Americanos (Lepidoptera) de Romualdo Ferriera D'Almeida (Nymphalidae: Ithomiinae) by Olaf H. H. Mielke & Keith S. Brown, Jr. Consehlo Nacional de Desenvolvimento Cientifico e Technologico, Curitaba, Parana, Brazil. 216 pp. 1979. No price stated.

These two volumes are an absolute necessity for anyone working in the family Ithomiidae (or subfamily Ithomiinae, depending upon your choice). At the time of his death in 1969 d'Almeida had completed the draft of his manuscript catalogue through names and articles published in 1968. Dr. Mielke, d'Almeida's scientific heir, sorted through the numerous manuscripts left to him and selected those for publication. This catalogue is one of them. It is another of d'Almeida's compilations of the literature on neotropical butterflies. The positions I have checked are accurate and complete in so far as he went, with a few exceptions that were caught by Mielke & Brown in their supplement.

The authors of the supplement have been involved in the study of this difficult family for some years. The supplement is a synopsis of their findings through the genus *Hypothryis* Hübner. This extends through p. 118 and covers the Tithorini, Melinaeini, and the Napeogenini, except for *Hyalyris* Bdv. Future work by this energetic team may be expected to complete these revisory studies. The few extended Portuguese notes in the catalogues are easily deciphered by those who do not command the language.

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CLEMENSIA ALBATA, AN ALGAL FEEDING ARCTIID[1]

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ABSTRACT.   The larva of *Clemensia albata* Packard (Arctiidae) feeds on an alga, *Protococcus viridis* Agardh, which grows on tree trunks. Observed maximum fecundity per adult female was 58 eggs. Minimum egg to adult time was 81 days, of which 47 were as larva. Feeding-resting cycles were dependent on humidity. Larvae were somewhat gregarious. The larva and pupa are described and illustrated.

Dyar (1904) and Huard (1929) reported lichens as the food plant for *Clemensia albata* Packard (Arctiidae: Lithosiinae). Huard's report may have been based on Dyar's findings, although he specified "les lichens des écorces." Dyar was able to rear one larva to second instar; however, there may have been enough free living algae present to account for this limited success. Larvae reared in the Catskill Mountains fed upon a green alga. According to Packard (1895), the larvae would not eat willow, poplar or lichens.

Forbes (1960) reported a South American lithosiine as feeding on a blue-green alga. No reference was given and Forbes may have received the information in correspondence, although Bourquin (1939) reported a lithosiine, *Eudesmia argentinensis* (Rothschild), as having "musgos y algos" as food plants although it was not clear that an alga was the actual host. Bourquin indicated that the food plant was growing on rocks in a humid environment, but he illustrated a larva browsing on a foliose bryophyte, probably a lichen. The plant was identified in the plates as *Hepatica* (= *Marchantia*), a liverwort. The aquatic larvae of some *Paragyractis* Lange (Pyralidae: Nymphulinae) live on algae-covered rocks in rapid streams. They spin webs on the rocks and the flattened larvae have blood gills near the spiracles (Munroe, 1972). Lange (1956) reported *Paragyractis jaliscalis* (Schaus) as feeding on algae and diatoms from rock surfaces on stream bottoms.

The ova of *C. albata* are creamy-white, spherical, with the base scarcely flattened, and are laid singly or in clumps of four or five. Dyar (1904) reported the egg diameter as 0.8 mm. Each egg is covered with a loose assemblage of scales from the tip of the female's abdomen. A particularly large, fresh female laid 58 eggs over the course of a week. Considering the large size of the egg, this is an impressive number for such a small moth.

Using specimens from the Adirondack Mountains, I started eight

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larvae on a lichen, *Hypogimnium* sp., and one larva developed to second instar, although it was never actually observed feeding (bits of bark were also present). On a second attempt, using Catskill material, first instar larvae were offered bits of bark, lichens, and a green alga, *Protococcus viridis* Agardh (Chlorophyta: Protococcaceae). The first instar larvae immediately congregated on the alga and refused to feed on the lichens even when the alga was removed.

Protococcus viridis grows on moist bark of trees, on old wood in subaerial habitats, and on floating logs (Prescott, 1962). In the Catskills, *P. viridis* had the best growths on the smooth trunks of *Acer rubra* L., *Betula lutea* Michx., and *B. lenta* L., especially those trees growing alongside the creek where the relative humidity was high. The algal host was difficult to gather in sufficient quantities for 58 larvae and all but 20 were released. The alga was gathered by stripping sections of birch bark. The best time to replenish the food was in the early morning, when the previous night's condensation had stimulated algal growth.

The larvae reared in the Catskill Mountains, Greene Co., New York, were offered *Hypogimnium* sp. and *Parmelia* sp., both lichens, but would not feed on these despite the fact that algae is the host half of the symbiotic relationship. Hale (1961) lists the following green algae as lichen symbionts: *Trebouxia, Myrmecia, Chlorosarcina, Coccomyxa, Chlorella, Trochiscia, Palmella, Protococcus, Leptosira, Phycopeltis,* and *Trentopohlia;* black or brown lichens contain blue-green algae (Cyanophyta), primarily *Nostoc, Gloeocapsa, Stigonema,* and *Rivularia.* In the case of *Parmelia* lichens, *Protococcus* is the algal symbiont.

The larvae of *C. albata* were found to feed at any hour, irrespective of light and dark periods, but dependent on relative humidity. Under dry conditions, the algal host is reduced to a thin, closely adhering layer of single cells on the bark. During humid weather, the alga multiplies and in a short time many layers of cells develop. Larvae are actively searching or feeding during humid periods. In the laboratory, the larvae would search for food after a few drops of water were added, even if no alga was provided. During periods of drought, the larvae crawl under bark and become inactive, although this inactive state is passive and can be terminated if disturbed. Unlike many lithosiines, *C. albata* immatures displayed no interspecific aggression. When it was dry, the larvae would congregate in parallel rows of five or six individuals even though there was adequate space and cover for solitary retreats. Pupae left in the petri plate with the larvae were not eaten. *Hypoprepia fucosa* Hübner and *H. miniata* Kirby have larvae which are cannibals on larvae and pupae. *Holo-*

melina aurantiaca Hübner will devour pupae of its own or of another species' as will numerous other arctiines.

The larval mandible, in many lithosiines, has a basal mandibular process; this is particularly prominent in *C. albata* (Fig. 7). Gardner (1943) referred to this process as a mola and thought it was a specialization for lichen feeding as the molae grind upon each other and might thereby serve to break up the indigestible outer coat of the fungal tissues. Whether the presence of a molar process is diagnostic for the subfamily remains to be seen. Gardner observed it in three genera and five species of Indian lithosiines.

Clemensia albata larvae have a disruptive pattern making them difficult to detect when they are feeding on the exposed surface of algae-covered bark. The black markings are produced by fine cuticular setulae which occur in definite patches. Subcuticular pigmented areas produce a pattern of brown blotches and a green body color provides the background. The caterpillars are sluggish and depend on their cryptic markings to avoid predators, in contrast to many arctiines which are fast crawlers and will quickly drop or roll into a ball when disturbed.

Pupation takes place under bark or in a furrow on the bark. A flimsy cocoon is constructed with bits of bark, algae, and a few strands of silk. Based on adult collection records, the species probably overwinters as a second or third instar larva. October and early spring records for the southern United States (Forbes, 1960; Kimball, 1965) indicate a potential for multivoltinism which the present study confirms.

Ova laid 8 July 1978 hatched eight days later. The first pupa was formed on 2 September, and the first adult emerged 28 September. The female moth (P1), larvae, pupae, and reared adults (F1) are associated by code number tlm 78-58. The description is based on ultimate instar larvae. Setal terminology follows Hinton (1946).

Description of *Clemensia albata*

Larva. Head 0.81 mm wide. Total length (fully expanded, preserved) 11–17.5 mm ($N = 12$, $\bar{x} = 15.35$). Abdominal prolegs present on third through sixth segments; crochets homoideous. Integument clothed with setulae (approximately $65/0.1$ mm^2) visible at 100×. Primary setae borne on chalazae, 1 seta per chalaza except subventral setae share a common chalaza. Metathorax, Ab-3 and Ab-7 with setulae longer than normal, giving appearance of dark patches. Subcuticular pigmented areas also present. Spiracle Ab-8 0.10 mm high. **Coloration:** Ground color dark, mossy green, integument mottled with black and brown, the black areas caused by setulae and the brown patches resulting from subcuticular pigmentation. Metathorax, Ab-3 and Ab-7 with subdorsal dark areas produced by setulae. Ab-1, Ab-2, and Ab-8 with lateral dark areas also produced by setulae. Overall appearance very cryptic. **Head** (Fig. 1): Epicranial suture 0.81 times height of frons. Second adfrontal seta (Af-2) posterior to apex of frons, located midway to origin of adfrontal sutures. Vertex, ocellar region, area adjacent to adfrontals, and upper half of area between adfrontal and frontal sutures dark brown. Anterior portion
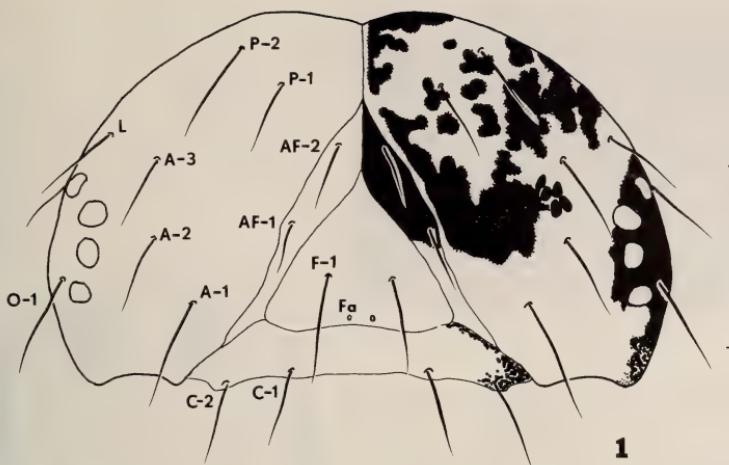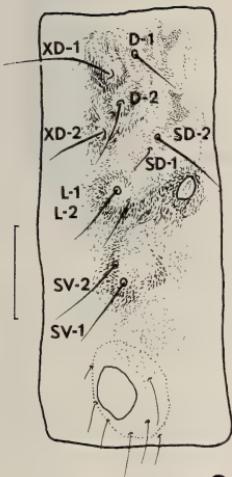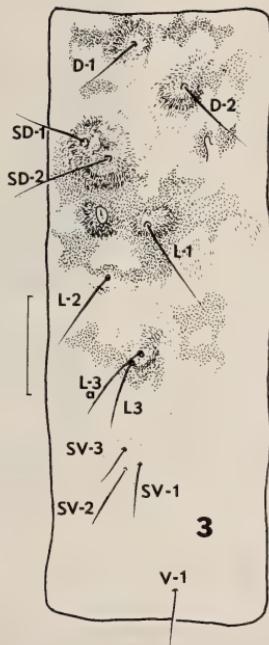
FIGS. 1–4. *Clemensia albata.* **1,** setal map and pattern of head; **2,** setal map of prothorax; **3,** setal map of 1st abdominal segment; **4,** setal map of 10th abdominal segment. Scale lines = 0.5 mm.

of head, frons, and clypeus, light, unpigmented. Posterior two-thirds of head capsule including apex of frons clothed with setulae visible under high power (100×). Ocellar interspaces between Oc1 & Oc2 and Oc2 & Oc3 subequal; Oc3 to Oc4 .5× diameter of Oc4. Oc4 to Oc6 2.6× diameter of Oc4; Oc4 to Oc5 2.75× diameter of Oc4. **Mouthparts:** Hypopharyngeal complex (Fig. 6): spinneret with distal lip surpassing second
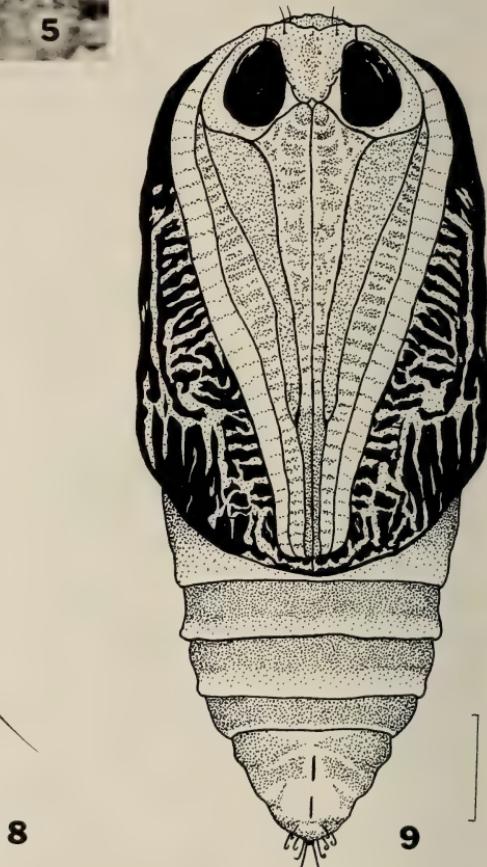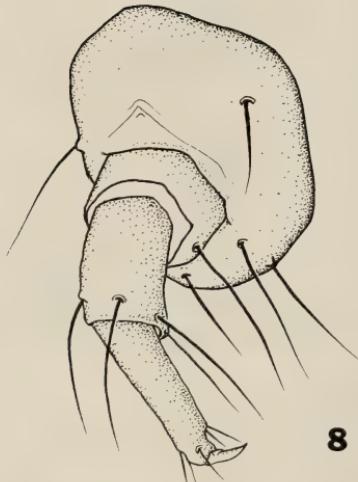
FIGS. 5–9. *Clemensia albata*. **5,** photograph of living larva; **6,** hypopharynx; **7,** mandible; **8,** thoracic leg; **9,** ♀ pupa containing pharate adult. Scale lines for Figs. 6–7 = 0.25 mm, for Fig. 9 = 1.0 mm.

segment of labial palpus, bare; stipular setae (S) short, half length of second segment of labial palpus. Distal and proximolateral region of hypopharynx without spines. Prementum weakly sclerotized, fading into distal region. **Mandible** (Fig. 7): Inner ridges not apparent; well developed molar process present at base. **Thoracic segments:** Prothorax (Fig. 2): cervical shield absent, setae borne on chalazae; integument clothed with setulae, dark patches occur where these setulae are longer; subcuticular pig-

mented patches present posterior to D1 and posterodorsal to SD2. D1 anterior to D2 and on its own chalaza; D2 posterior to and equidistant from XD1 and XD2; SD2 the most posterior of the primary setae and much larger than SD1 which is located antero-ventrad of SD2; L1 & L2 on a single chalaza; SV1 & SV2 on a single chalaza. 6 coxal setae present (Fig. 2). Spiracles pale. Meso- and metathorax: similar to prothorax, setae borne on chalazae; D1 & D2 share same chalaza as do D2 & XD2; SD2 weakly developed and SD1 strongly developed on meso- and metathorax; SD2 and SD1 farther apart than on prothorax, SD2 closer to D2 than to SD1. **Abdominal segments** (Figs. 3–4): Ab-1 (Fig. 3) with setae borne on chalazae. Markings produced by hairs and subcuticular pigmentation as with thoracic segments. SD1 & SD2 adjacent, but on separate chalazae; L1 & L2 distant, L1 nearly on horizontal and L2 nearly on vertical plane with spiracle; L3 chalaza bisetose; SV1, 2, & 3 and V1 all present. Segments protuberant dorsally. Crochets a uniordinal, homoideous mesoseries; 13–20 per third abdominal proleg (N = 12, x̄ = 17.38), 10–22 per fourth (x̄ = 17.04), 16–22 per fifth (x̄ = 17.87), and 13–19 per sixth (x̄ = 17.04).

Material examined: 12 specimens, Stony Clove Creek, elev. 412 m, lat. 42°08′00″, long. 74°15′10″, Greene Co., New York, larvae preserved 2 September 1978, from ova of female collected, determined and reared by T. L. McCabe.

Pupa. Female pupa (containing pharate adult): Two pairs of setae, one pair on each anterolateral corner of the frons as drawn. Compound eyes of imago visible through pupal case as drawn; glazed eye only partly covers actual eye, sculptured eye lies almost wholly over actual eye. Maxillae, second pair of legs, and antennae all project nearly to wing tip; first pair of legs extends two-thirds distance of maxilla; third pair of legs concealed. Wings with furrows as drawn. Lateral and dorsal surfaces of abdomen sparsely covered with microscopic, many branched setae (visible at 100×). Cremaster with two types of setae: 8 small, subapical setae with curled apices and 2 large, apical setae with reflexed apices. **Male pupa:** Same as the female except the gap between the anal and genital slit is greater, that of the male being twice the length of the anal slit whereas the gap in the female is subequal in length to the anal slit.

Material examined: 3 specimens, Stony Clove Creek, elev. 412 m, lat. 42°08′00″, long. 74°15′10″, Greene Co., New York, pupae preserved 5 October 1978.

ACKNOWLEDGMENTS

LITERATURE CITED

BOURQUIN, F. 1939. Mariposas Argentinas; vida, desarrolo, costumbres y hechos curiosos de algunos Lepidópteros Argentinos. Buenos Aires. 209 pp.

DYAR, H. G. 1904. Lepidoptera of the Kootenai District. Proc. U.S. Nat. Mus. 27: 779–938.

FORBES, W. T. M. 1942. Lepidoptera of Barro Colorado Island, Panama. Bull. Mus. Comp. Zool. 90(1): 169–187.

——— 1960. Lepidoptera of New York and neighboring states. Cornell Univ. Agric. Exp. Sta. Mem. 371(4): 41–50.

GARDNER, J. C. M. 1943. Immature stages of Indian Lepidoptera (5). Indian Jour. Ent. 5: 89–102.

HALE, M. E., JR. 1961. Lichen Handbook. Smithsonian Institution, Washington, D.C. 178 pp.

HINTON, H. E. 1946. On the homology and nomenclature of the setae of lepidopterous

larvae, with some notes on the phylogeny of the Lepidoptera. Trans. Roy. Entomol. Soc. Lond. 97: 1–37.

HUARD, V. A. 1929. Faune Entomologique de la Province de Québec, Sixieme Ordre, Les Lépidopteres Nocturnes. Le Naturaliste Canadien 55(12): 275–276.

KIMBALL, C. P. 1965. Arthropods of Florida and neighboring land areas, I: Lepidoptera of Florida, an annotated checklist. Gainesville, Florida. 363 pp.

LANGE, W. H., JR. 1956. A generic revision of the aquatic moths of North America: (Lepidoptera: Pyralidae, Nymphulinae). Wasmann J. Biol. 14: 59–144.

MUNROE, E. 1972. In Dominick, R. B. et al., 1972, The moths of America north of Mexico, Fasc. 13.1A, Pyraloides (in part). 134 pp.

PACKARD, A. S. 1895. Early stages of some bombycine caterpillars. J. N.Y. Entomol. Soc. 3: 175–180.

PRESCOTT, G. W. 1962. Algae of the western Great Lakes area. W. C. Brown, Dubuque, Iowa. 977 pp.

HEMILEUCA GROTEI (SATURNIIDAE): ITS MORPHOLOGY, NATURAL HISTORY, SPATIAL AND TEMPORAL DISTRIBUTION[1]

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ABSTRACT. The life history, including descriptions of immatures, illustrated last instar larva and adult genitalia, the larval foodplants utilized, parasites, predators, habitat characteristics, flight periods, and known range, are given for *Hemileuca grotei* Grote & Robinson.

The small saturniid moth, *Hemileuca grotei* Grote & Robinson, remains poorly known, and material is rare in private and museum collections. It is thus our primary purpose to provide information to help collectors obtain specimens from the field and to expand on the excellent treatment of this species given by Ferguson (1971). McDunnough (in Packard, 1914) stated that Kerrville is the type locality, but we are unable to substantiate this statement. The type material was collected in central Texas by Otto Friedrich (1800–1880), a German who spent much of his life studying Lepidoptera of the region (Geiser, 1932). The types may have come from New Braunfels or near there (Guerne) where Friedrich lived and collected for many years (Geiser, 1932).

In the earlier literature *H. grotei* was much confused with *Hemileuca diana* Packard (e.g., Schuessler, 1934). The pair figured in Packard (1914) on Plate 63 as *H. grotei* is actually *H. diana*. Claude Lemaire (Paris Museum) has kindly sent us material of *H. diana* from Santa Cruz Co., Arizona, reared from larvae collected on *Quercus oblongifolia* Coulter, Fagaceae. This species is larger and browner than *H. grotei* with better developed light bands. Ferguson (1971) reported *H. diana* from Texas based on 2 old specimens with vague data in the American Museum of Natural History. The occurrence of this species in Texas needs verification with further collecting. Re-

ports in older literature of *H. grotei* occurring in Colorado and Arizona apparently all refer to *H. diana.*

Geographical Distribution and Biotope

Outside of Texas, *H. grotei* has been authentically recorded in the literature only from Jemez Springs, Sandoval Co., and Maxwell, Colfax Co., New Mexico (Ferguson, 1971). We add the following new county records for Texas: Bandera, Blanco, Burnet, Comal, Coryell, Eastland, Hamilton, Johnson, Kimble, Lampasas, Llano, Mills, Motley, Palo Pinto, Pecos?, San Saba, Taylor, Travis, and Williamson. Kilian Roever (pers. comm.) informed us that he has it from Burnet, Johnson, and Palo Pinto counties, and that he was unsuccessful in rearing larvae (*H. grotei* ?) found on *Quercus mohriana* Buckley from Pecos Co. Specific data were not provided, and we have not seen specimens from Palo Pinto or Pecos counties. It is possible that *H. grotei* occurs in southwestern Oklahoma. Spatial and compressed temporal distributions of *H. grotei* in Texas are shown in Fig. 1 (map).

In the lab, larvae accept many oak species except *Quercus nigra* Linnaeus. In nature the principal oak species utilized in Texas is *Q. fusiformis* Small, which grows commonly over much of central Texas. This tree has been confused taxonomically with *Q. virginiana* Miller which grows in coastal Texas, outside the range of *H. grotei*, and therefore does not serve as an oviposition substrate for females. We have found ova and larvae on *Q. havardii* Rydberg × *Q. stellata* Wangenheim, *Q. texana* Buckley, and *Q. marilandica* Muenchhausen, and they are probably selected by ovipositing females in that order. In vegetative overlap areas, relative abundance of these oaks is in the same order. Oviposition is probably not random on any of them.

In Texas, *Hemileuca grotei* is limited on the southern and southeastern boundaries of its range by the Balcones Escarpment where it is well established. Here the biotope is characterized by rolling limestone hills and scrubby oaks. To the northwest, in the High and Rolling Plains areas of the state, its distribution is poorly known. Here the biotope is characterized by scrubby, mostly shinnery, oaks growing in deep sand. Most of the land is privately owned, fenced, and used for grazing livestock. We have found, however, that by working along public roads, and in State Parks, one can obtain a good cross section sampling of the area being studied. More definitive habitat characteristics must await a better knowledge of the species through more extensive and detailed field studies, especially in the northwestern part of its range.

The occurrence of *H. grotei* in certain parts of the state undoubtedly has been altered through land development. In the late 1930s vast
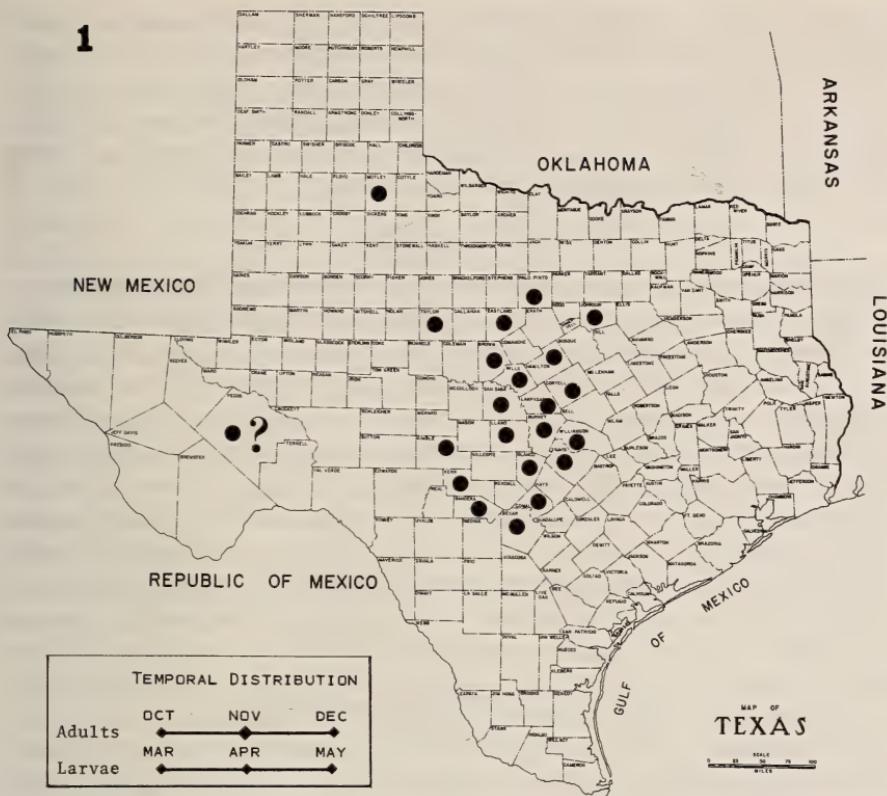
Fig. 1.   County map of Texas showing known or reported locations for *H. grotei*.

areas of shinnery oak, *Q. havardii*, grew in the area west and south of Lubbock (Tharp, 1939). At that time this area was known as the Sandy South Plains. Today it is represented as the southwestern portion of the High Plains or vegetational area 9 of Correll & Johnston (1970). Since then irrigation has come to the area, and much is under cultivation; however, some isolated areas still exist on both sides of the Texas/New Mexico state line. We believe that with careful searching *H. grotei* could be found in these undisturbed areas. To the east of this area, the most promising section is along the north-south line dividing the High and Rolling Plains vegetational areas (Correll & Johnston, 1970). Here the Cap Rock Escarpment divides the 2 areas, and along this line in deep sand one will find shinnery oak, *Q. havardii*, and also *H. grotei*. Shinnery oak may be found at various other locations almost throughout the Rolling Plains area. The interested collector would be well advised to search these areas carefully.

It appears to us that the overall or composite biogeographical habitat of *H. grotei* is climatologically intermediate between *H. maia* (Drury) (humid eastern) and *Hemileuca oliviae* (Cockerell) (dry or semi-arid western). We do not know enough about the biology of *H. diana* to say where it fits into the biogeographical picture, but we do have doubts that it currently exists in Texas.

Field Observations

Locating egg masses on oak branches is difficult for several reasons: the egg rings contain considerably fewer eggs than those of *H. maia* and *Hemileuca nevadensis* Stretch; the evergreen foliage of *Q. fusiformis* and the dead, brown, persistent leaves of *Q. texana* provide additional camouflage; the deciduous *Q. havardii* provides greatest visibility, but *H. grotei* is less common on this tree. Unless the collector is especially interested in studying the eggs, it would be far more expedient to wait until about mid-March and search for larvae. At the southern limit of its range, eggs of *H. grotei* hatch in early March. One observed hatching was 10 March. The exact time will vary from year to year throughout its range depending on the climate for a given season. Based on recently hatched egg masses without finding larvae, we have reason to believe that from time to time, unseasonably warm days in certain parts of the range may cause premature hatching of eggs, and the young larvae die for lack of food. Although egg shells frequently remain on the twigs for several seasons, we distinguish between current and prior year hatchings.

Larvae are best collected while still gregarious in the early instars. At this time they are black, more easily seen, and are less likely to be parasitized. In the later instars larvae disperse across the ground to other trees, their color pattern changes, and they are better camouflaged. Larvae are not generally difficult to bring to pupation in captivity. Cut oak branches placed in water will remain fresh for some time. For best results the branches should be placed in large containers with a screen or cloth covering to allow good air circulation, to prevent escape, and to keep out parasites.

In the search for immatures, one should direct his activities to oak clumps, semi-isolated shrubs, or small trees with a southern or southwestern exposure. It is in spots such as this that females deposit their eggs on twigs at various levels on the trees. Some are low, well within reach of the collector, while others are beyond his reach. When the eggs hatch, the young larvae move gregariously to the terminal end of the branch where they feed on the new growth. At this time they are easy to find.

Although some of our data are based on reared material removed

from the source locality, we see a general pattern that eggs eclose earlier, and adults fly later, in the southern part of the range. Specifically, in Bexar Co. larvae will mature by early May, but not until mid- or late May in Eastland Co. Adults fly in mid- to late November in the southern areas and in late October to mid-November in Brown, Eastland, and Mills counties. All of these times will vary according to weather conditions for the particular year. Some pupae do not yield adults until the fall of the following or even the second year after pupation. The overall flight period in Texas, based on data at hand, is from late October to late November, peaking about mid-November.

As with some other species of *Hemileuca*, the adults emerge during the morning (ca. 0930 h Central Standard Time). A male was observed in Mills Co. by Peigler on 29 October in flight at 1232 h. Kendall has observed adults flying from mid-morning to mid-afternoon. The flight is rapid, and the red anal tuft of the males is visible only when hovering to alight. Frequently on cool days before the sun warms the earth's surface or on very cloudy days, adults may be found hanging to oak twigs and can be collected directly into the killing jar. Adults do not come to artificial light.

Parasites, Predators, and Disease

Parasites

The incidence of parasitism appears to be high, although we find no previously published records for parasitism of *H. grotei;* larvae may be parasitized by Hymenoptera, but we have found only Diptera. Three of the four parasites found are parasitic on other Lepidoptera species as indicated below. Parasitized larvae grow until the time for pupation when they suddenly die instead of pupating. The parasite larvae then leave the host to pupate, usually in the ground; if denied soil in which to pupate, adults may not eclose later. Eggs of tachinids can be seen adhering almost anywhere on the body of the caterpillar, but they are often on the prolegs, even on the crochets. We give here the specific parasites observed.

Tachinidae. *Leschenaultia fulvipes* (Bigot), 21 mm wing expanse, brownish black puparium; Bexar and Eastland counties. Arnaud (1978) cited other Lepidoptera hosts as: *Malacosoma californicum* (Packard), *M. californicum fragile* (Stretch), *M. incurvum incurvum* (Hy. Edwards); *Hemileuca lucina* Hy. Edwards, and *H. maia* (Drury). *Exorista mella* (Walker), 20–24 mm wing expanse, blackish puparium, one to several per host larva; Brown, Eastland, and Motley counties. Watts & Everett (1976) recorded *H. oliviae* as a host. Arnaud (1978) cited many other Lepidoptera species in some 10 different families

that are hosts for this parasite. *Spoggosia* sp., 10 mm wing expanse with a red-brown puparium, 1 or 2 per host larva; Mills Co. Arnaud (1978) cited only *Spoggosia gelida* (Coquillett); it probably parasitizes the pupa of *Dasychira* spp. These 3 Tachinidae were determined by C. W. Sabrosky, Systematic Entomology Laboratory, United States Department of Agriculture.

Phoridae. *Megaselia* sp., this very small fly was found infesting diapausing pupae from Eastland Co. in the lab at San Antonio, Bexar Co. Determination was by W. W. Wirth, Systematic Entomology Laboratory, United States Department of Agriculture.

Predators

Undoubtedly the larvae and pupae of *H. grotei* are preyed upon by many different insects (especially wasps), spiders, birds, and mammals, but we are aware of but 2 at this time: 1) a large brown stinkbug *Apateticus cynicus* (Say), Pentatomidae (both nymphs and adults), determined by Joe E. Eger, Texas A&M University; and 2) the well known *Calosoma scrutator* Fabricius, Carabidae, which is well established over much of the range of *H. grotei* (Both the larva and adult beetle are predaceous on caterpillars.).

Disease

Mutually independent field trips made by us on 7, 8, 16, and 18 April 1979 disclosed larvae of *H. grotei* in abundance at both new and previously visited sites. Although several hundred larvae were collected by us over a wide area (11 counties), few survived. Most larvae appeared to have died of an unidentified virus or bacterium. Some larvae would become limp and then simply "melt" away. Other larvae would first become rigid and then become covered with a mold-like fungus, the "spores" spreading to nearby leaves covering them with a greyish powder. From ca. 150 larvae collected in 4 counties by Kendall, and reared under conditions which had proven most successful previously, 3 pupated, 3 died of parasitism, and the remainder seemingly died of a virus or bacterium. These organisms appear to have affected larvae of other Lepidoptera in the same way. Many geometrid larvae were collected with the result that all but 2 died before pupating. It was significant to note that most of the larvae collected by Kendall were either on the ground or resting on ground-cover vegetation. Few were feeding in nature, and very little feeding occurred in the lab. Although no dead larvae were found in the field, several larvae were rejected because they were unusually limp when handled. Later, several noctuid larvae feeding in the wild (in the lab

garden) were found dead and disintegrating, but still clinging to vegetation.

We are inclined to attribute the disease to unusually humid conditions early in 1979; high humidity which persisted for a long time, and extended over much of the Edwards Plateau. Rainfall at San Antonio, for example, was ca. 35 cm by 1 May as compared to a normal of 20 cm. We have found the larvae of certain other saturniids very sensitive to humidity. If the larvae of *Hemileuca chinatiensis* (Tinkham), *H. oliviae*, or *Agapema galbina* (Clemens) are moved from their naturally arid habitat to San Antonio, Texas, where the humidity is low by most standards but high compared to that of the natural habitat of these species, most if not all will soon die of this undetermined disease; we have experienced such results even when the larvae were reared in an outdoor environment.

Texas Specific Field and Lab Records

Some of the specimens cited remain in the collections of the authors, but most of them are in various natural history museums, and private collections throughout the United States, and in Europe.

Bandera Co., nr. Bandera: 25 November 1978 (1 ♂), Edward V. Gage. Bexar Co., nr. Helotes: 17 November 1962 (1 ♂), 19 November 1962 (1 ♂), 1 November 1963 (1 ♂), 16 November 1963 (1 ♀), all *ex larvis*, found on *Quercus fusiformis* and reared on *Q. shumardii* Buckley, Roy W. and Ellen S. Quillin; 17 November 1963 (18 ♂, 2 ♀) Roy O. and C. A. Kendall; 11 November 1964 (2 ♂, 1 ♀), 12 November 1964 (1 ♀), 13 November 1964 (1 ♂), 14 November 1964 (3 ♀), 15 November 1964 (2 ♂, 1 ♀), 16 November 1964 (1 ♀), 17 November 1964 (2 ♀), 24 November 1964 (2 ♀), 12 November 1965 (1 ♂), 19 November 1965 (1 ♂), 20 November 1965 (1 ♀), 26 November 1965 (1 ♀), all *ex ovis*, *Q. fusiformis*, Roy O. and C. A. Kendall (4 of these did not emerge until the year following pupation); San Antonio (Kendall lab garden): 19 April 1979, 3 larvae, *Q. fusiformis*, all seem to have succumbed to disease.

Blanco Co., Pedernales Falls State Park: 8 April 1979, few disbursed larvae on *Q. fusiformis*, R. S. Peigler; Hwy 281, ca. 10 km S of Johnson City: 18 April 1979, 11 larvae, *Q. fusiformis*, all seem to have succumbed to disease, Roy O. and C. A. Kendall.

Brown Co., Lake Brownwood State Park: 9 April 1964 (3rd instar larvae, *Q. fusiformis*), adults emerged 18 November 1964 (1 ♀), ca. 25 December 1964 (1 ♂); 11 April 1978 (larvae, *Q. fusiformis*), pupated 15–26 May 1978, adults emerged 16 October 1978 (1 ♀), 17 October 1978 (2 ♀), 20 October 1978 (1 ♂), 21 October 1978 (1 ♂), 22 October 1978 (1 ♂), 23 October 1978 (1 ♂), 22 January 1979 (1 ♂), 19 October 1979 (2 ♀), 25 October 1979 (1 ♀), 26 October 1979 (1 ♀), 27 October 1979 (1 ♂, 2 ♀), 31 October 1979 (1 ♂), 1 November 1979 (1 ♂) (10 emerged the year following pupation), all Roy O. and C. A. Kendall.

Burnet Co., Inks Lake State Park: 7 April 1979, larvae abundant on *Q. fusiformis* (collected many); Hwy 281, ca. 4 km S of Burnet: 8 April 1979, few larvae on *Q. fusiformis;* Inks Lake State Park: 18 April 1979, ca. 200 mature larvae, 3 larvae on *Q. stellata*, the remainder on *Q. fusiformis*, all R. S. Peigler.

Comal Co., Hwy 281, nr. Spring Branch: 18 April 1979, 3 larvae on *Q. fusiformis*, all seem to have succumbed to disease, Roy O. and C. A. Kendall.

Coryell Co., Hwy 84, ca. 5 km W of Purmela: 18 April 1979, 5 larvae on *Q. fusiformis*, R. S. Peigler.
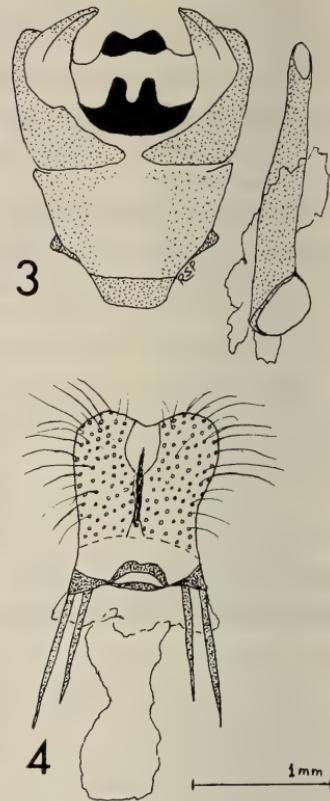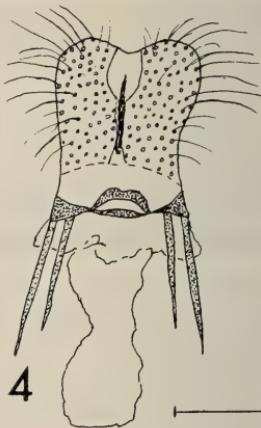
FIGS. 2–4. *Hemileuca grotei.* **2,** Mature larva; **3,** Male genitalia; **4,** Female genitalia.

Eastland Co., nr. Eastland: 13 May 1973 (numerous last instar larvae, *Q. fusiformis*), larvae pupated 18–25 May 1973 and adults emerged 26 October 1973 (4 ♂), 29 October 1973 (2 ♀), 30 October 1973 (1 ♂), 22 October 1974 (2 ♀), 23 October 1974 (1 ♂), 31 October 1975 (1 ♀) (3 emerged 1 year and one 2 years following pupation), Roy O. and C. A. Kendall.

Hamilton Co., Hwy 84 at Lampasas River: 18 April 1979, larvae on *Q. fusiformis*, R. S. Peigler.

Kerr Co., Kerr Wildlife Management Area nr. Hunt: 17 April 1965 (few larvae, *Q. fusiformis*), 1 pupated ca. 13 May 1975 and a ♀ emerged 5 November 1965, Roy O. and C. A. Kendall; ca. 11 km SW of Kerrville: 5 November 1902 (1 or more), 7 November 1902 (1 ♀), 9 October 1904 (1 ♀), the last 2 *ex larva*, Howard G. Lacey (Kendall & Kendall, 1971).

Kimble Co., Hwy 290, ca. 11 km W of Harper: 27 April 1979, few larvae, *Q. fusiformis,* Joe E. Eger.

Lampasas Co., nr. Lometa: 17 April 1975 (few larvae, *Q. marilandica*), 4 pupated before 10 May 1975, adults emerged 23 October 1975 (1 ♂), 4 November 1975 (1 ♀), 22 November 1976 (1 ♀) (1 emerged the year following pupation), Roy O. and C. A. Kendall.

Llano Co., Enchanted Rock Park, ca. 32 km N of Fredericksburg: 7 April 1979, few larvae on *Q. fusiformis*, R. S. Peigler; Hwy 71 rest area, ca. 16 air km S of Kingsland:

18 April 1979, ca. 60 larvae (mostly on ground beneath *Q. fusiformis*), 2 were parasitized, 3 others pupated 24 April 1979 (2), 26 April 1979 (1), the remainder died, probably of a virus, a ♂ emerged 1 November 1979, and 2 pupae remained in diapause as of 18 January 1980, Roy O. and C. A. Kendall.

Mills Co., ca. 13 km S of Goldthwaite: 17 April 1975 (larvae, *Q. fusiformis*), pupated 10–14 May 1975, adults emerged 17 October 1975 (1 ♂), 28 October 1975 (1 ♀), 1 November 1975 (1 ♀), 8 November 1975 (1 ♀), Roy O. and C. A. Kendall; nr. Goldthwaite: ? May 1977, 31 larvae feeding singly on *Q. havardii × stellata, Q. texana,* and *Q. fusiformis,* R. S. Peigler; 8 km W of Goldthwaite: 18 April 1979, few larvae on *Q. havardii × stellata,* R. S. Peigler.

Motley Co., ca. 10 km W of Roaring Springs: 14 May 1977 (1 last instar larva, *Q. havardii × Q. stellata*), parasitized, Roy O. and C. A. Kendall.

San Saba Co., Hwy 16 nr. San Saba: 18 April 1979, 1 parasitized larva on *Q. fusiformis,* R. S. Peigler.

Taylor Co., ca. 13 km S of Merkel: 3 November 1943 (1 ♂), 4 November 1943 (1 ♂, 1 ♀), Charles L. Remington.

Travis Co., Hwy 71 rest areas ca. 11 and 19 km WNW of Bee Cave: 16 April 1979, many larvae (ca. 60 collected) eating *Q. fusiformis* and *Q. texana,* all died, probably of a virus, Roy O. and C. A. Kendall.

Williamson Co., Hwy 29, vicinity of Liberty Hill: 18 April 1979, larvae abundant on highway, many killed by passing motorists, R. S. Peigler.

Morphological Descriptions

Apparently the larva and pupa of *H. grotei* have not been described previously. The pupal description utilizes work of Mosher (1914, 1916) with her descriptions and figures of pupae of other species of *Hemileuca.* Ferguson (1971) gave a good figure of the male genitalia; the female genitalia are figured here and described for the first time. The descriptions below are compared to *H. maia* from Baton Rouge, Louisiana. The male antennae of *H. grotei* have ca. 36 segments; those of *H. maia* have ca. 44 segments. (These counts are based on one male of each species.)

Mature larva (Fig. 2). Head 4.5 mm wide, rusty brown with numerous blackish mottles and sparse white setae. Thoracic legs stramineous. A lateral whitish stripe connecting subspiracular scoli. Integument maroon with numerous oval cream-colored flecks. Ventrum, prolegs, and intersegmental areas dull orange. Scoli all about equally developed, unlike *H. maia* in which the 2 dorsal rows of scoli are shorter, rust-colored tufts; black stalks with whitish branches which are distally darkened. Spiracles cream-colored. Overall aspect more like *H. burnsi* Watson than *H. maia.* Length 49 mm.

Pupa. Color black-brown as in *H. maia.* Cremaster with 6 spikes, same as *H. maia.* (These counts made from 19 *grotei* and 17 *maia* pupae.) Pro- and mesothoracic legs longer and narrower on pupal shell than *H. maia.* Otherwise very closely resembling *H. maia.* Length 22 mm.

Male genitalia (Fig. 3). Overall structure roughly half as large as *H. maia.* The costal lobe of the valve is more slender and less sclerotized than that of *H. maia.* Gnathos heavily chitinized and more strongly bifid than in *H. maia.* Uncus with less-produced lobes. Anellus membranous (sclerotized in *H. maia*). Aedeagus two-thirds the size of that of *H. maia.*

Female genitalia (Fig. 4). Genital plaque more chitinized than in *H. maia.* Proctiger slightly longer but only half as wide as in *H. maia.* Numerous long setae on proctiger each with a basal button. Apodemes tapering to a sharp point. Posterior apodemes long; anterior pair shorter.

ACKNOWLEDGMENTS

LITERATURE CITED

ARNAUD, P. H., JR. 1978. Host-parasite catalog of North American Tachinidae. United States Dept. Agric. Misc. Publ. 1319. 860 pp.

CORRELL, D. S. & M. C. JOHNSTON. 1970. Manual of the vascular plants of Texas. xiii + 1881 pp. Texas Research Foundation, Renner, Texas.

FERGUSON, D. C. 1971. Bombycoidea, Saturniidae (in part), in R. B. Dominick et al., The moths of America north of Mexico, fasc. 20.2A: 1–153, pls. 1–11. E. W. Classey, London.

GEISER, S. W. 1932. Naturalists of the frontier. Southwest Review 17: 421–460.

KENDALL, R. O. & C. A. KENDALL. 1971. Lepidoptera in the unpublished field notes of Howard George Lacey, naturalist (1856–1929). J. Lepid. Soc. 25(1): 29–44.

MOSHER, E. 1914. The classification of the pupae of the Ceratocampidae and Hemileucidae. Ann. Entomol. Soc. America 7: 277–300.

——— 1916. The classification of the pupae of the Saturniidae. Ann. Entomol. Soc. America 9: 136–158.

PACKARD, A. S. 1914. Monograph of the bombycine moths of North America, part 3 (T. D. A. Cockerell, ed.). Mem. Natl. Acad. Sci. 12: ix + 1–276 + 503–516, 34 figs., 113 pls.

SCHUESSLER, H. 1934. Saturniidae, in E. Strand, Lepidopterorum Catalogus, pars 58: 325–484. W. Junk, Berlin.

THARP, B. C. 1939. The vegetation of Texas. Texas Acad. Sci. Publ. in Nat. Hist., Nontech. series 1: xvi + 74.

WATTS, J. G. & T. D. EVERETT. 1976. Biology and behavior of the range caterpillar. New Mexico State Univ. Agric. Exp. Sta. Bull. 646: 1–32.

A PRELIMINARY INVESTIGATION OF EMBRYONIC INBREEDING DEPRESSION IN TWELVE SPECIES OF LEPIDOPTERA

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ABSTRACT. Inbred (sib-sib) matings were made in population cultures of twelve species of Lepidoptera (*Boloria bellona, B. selene, Phyciodes tharos, P. batesii, P. campestris, Junonia coenia, Pararge aegeria, P. megera, Pieris rapae, Arctia caja,* and *Cisseps fulvicollis*) and the resulting loss of egg hatchability was compared with control, outbred matings in the same cultures. A relatively extensive series of inbred matings within a single population of *Phyciodes tharos* revealed that embryonic genetic load is composed of very few, strongly deleterious genetic units. This seems to be true of all of the lepidopteran species tested. Genetic load values for nine of the species seemed homogeneous and varied between 0.5 and 2.0 lethal equivalents per zygote. There was only a single value for the tenth species; this may be anomalous. Two species of the group seem to have significantly lower and higher genetic loads than the other species. This may be a result of differences in population structure.

Genetic variation within populations and species theoretically has a highly adaptive role in enabling the organism to respond to varying environmental stress (e.g., Dobzhansky, 1970). However, a portion of this variation (the "genetic load") consists of genes that, when expressed, result in a loss of fitness for the carrier. Since segregation and recombination in sexual, non-selfing organisms lead inevitably to the production of disadvantageous homozygotes, each population presumably must strike a balance between population size and structure (and thus levels of inbreeding) on the one hand and size of the genetic load on the other. Under conditions such as the laboratory, where close inbreeding suddenly becomes the rule, genetic load is expressed as inbreeding depression. Comparative studies on inbreeding depression in different species and populations within species should provide information on the composition of genetic loads and eventually enable some general inferences to be drawn on the species' natural levels of inbreeding and population structure. This paper represents a preliminary attempt to estimate genetic loads for a small, heterogeneous group of lepidopteran species.

The magnitude of the genetic load in a population is usually estimated by observation of the reduction from normal survivorship during a given sensitive period (i.e., during a time of rapid tissue development and growth) in development of progeny from a series of matings of a known degree of inbreeding. This approach has been used for populations of *Drosophila* (e.g., Dobzhansky et al., 1963), Douglas-fir (Sorenson, 1969), humans (Morton et al., 1956), and domestic animals (Pisani & Kerr, 1961; Sittmann et al., 1966). A second method has been used for *Drosophila*. This uses genetic markers as

a means of estimating the frequencies in a population of chromosomes bearing lethal and sublethal genes. When both methods are used simultaneously on the same *Drosophila* populations (e.g., Dobzhansky et al., 1963; Malogolowkin-Cohen et al., 1964) the former method gives a consistently lower result, indicating synergism among the components of the load. Because of this synergism, estimates of load magnitude made under conditions of intense inbreeding can be considered only as relative values. However, the intensity of inbreeding in the present experiments was less than that necessary to produce significant synergism (Kosuda, 1972) and should reflect actual levels of genetic load.

During the course of breeding work involving maintenance of twelve species of Lepidoptera (*Boloria bellona bellona* Fab., *B. selene* Schiffermüller (ssp. *myrina* Cramer and *sabulocollis* Kohler), *Phyciodes tharos tharos* Drury, *P. tharos pascoensis* Wright (probably best considered a separate species (Oliver, in prep.)), *P. batesii* Reakirt, *P. campestris* Behr (ssp. *montana* Behr), *Junonia coenia coenia* Hübner (all Nymphalidae); *Pararge aegeria* L. (ssp. *tircis* Butler), *P. megera megera* L. (Satyridae); *Pieris rapae rapae* L. (Pieridae); *Arctia caja caja* L. (Arctiidae); and *Cisseps fulvicollis* Hübner (Ctenuchidae)) at various times during a period of ten years, I took the opportunity of making observations on control and inbred broods reared under the same conditions and usually simultaneously. I have made estimates of the magnitude of genetic load in each population culture from a comparison of survivorship of progeny from control and inbred matings. In these species by far the greatest expression of genetic load occurs during embryonic development (Oliver, unpub. data). Data on embryonic survivorship is also much easier to gather than that on later life stages. For these reasons this paper considers only embryonic viability among the twelve species.

Unfortunately, there is little hard data on the population structure of these species. *P. t. tharos* has a wide range of habitats and is generally abundant; there is good evidence for near panmixis over the eastern United States (Vawter & Brussard, 1975). *P. t. pascoensis* is more habitat-restricted and tends to show significant population differentiation (Oliver, in prep.); *P. c. montana* probably has a similar population structure. *P. batesii* in the northeastern United States occurs in small, highly isolated populations (Oliver, 1979). My field observations indicate that *P. megera* (Oliver, 1972b) and *P. aegeria* show little individual motility and tend to occur in localized populations, as do *B. selene, B. bellona,* and *C. fulvicollis.* *A. caja* is common and general in central Europe; *P. rapae* is abundant in almost all open areas in the eastern United States. *J. coenia* is a highly vagile

species that tends to form large colonies which may often be founded by single fecundated females (e.g., Shapiro, 1978).

Almost nothing is known about the composition of the genetic load in Lepidoptera. If the heterozygosity involved in genetic loads is similar to the great genic variation that has been observed in natural populations of most organisms (Lewontin, 1974; Richmond, 1972), including butterflies (Burns & Johnson, 1967), then the chances are very small of picking at random even two parents having a level of variation differing significantly from the population average. The data of Dobzhansky et al. (1963) seem to support this view; no correlation was found between viability and pedigree in a long series of inbred *Drosophila* cultures. However, when lethals or semilethals are involved, very high levels of inbreeding depression may be due to the actions of only a few genes.

METHODS

One to six cultures were maintained for each species. Detailed information on culturing techniques has been given in earlier papers (Oliver, 1972a, 1972b, 1977, 1978, 1979). Each culture was begun from parents caught in a separate locality. Embryonic survivorship in the progeny from inbred matings between siblings (coefficient of inbreeding, F, = .250) was compared with that from control, outbred intrapopulation matings ("combined controls" in Table 1). In each case the siblings used were the progeny of an outbred (usually wild) intrapopulation mating having normal hatchability.

Each of the cultures was begun with a comparatively small number of wild parents, from 2 to 22. Because of uncertainty regarding the reliability of data from very small population samples, the program was carried out in two parts. The first (Part A) consisted of observations on cultures of all species maintained from 1968 to 1978, the second (Part B) of a more systematic set of inbred matings made during 1973 and 1975 using a population of *Phyciodes tharos* from western Pennsylvania. In this part six isofemale families were established and 9 to 14 successful sibling pairings made within each family. An additional two families (73-23 and 73-31) were derived by outcrossing the F_1 progeny of the original wild parents of these families. Sib matings were then made within each of these two additional families.

Cultures were begun from individuals caught at the following localities:

Boloria b. bellona—MASSACHUSETTS: Acton, Middlesex Co.; PENNSYLVANIA: Forward Twp., Allegheny Co.
B. selene myrina—MASSACHUSETTS: Acton, Middlesex Co.
B. s. sabulocollis—SOUTH DAKOTA: Custer Park, Custer Co.

TABLE 1. Mean hatchability of eggs and embryonic genetic loads (L. E./zygote) in control and inbred lines of Lepidoptera. Coefficient of inbreeding (F) = 0 for controls (c); (F) = .250 for inbred (i) broods.

Species & provenance	No. of broods	No. of wild parents	No. of eggs	Colored/laid[1,2]	Hatched/laid[2]	L. E./zygote
B. bellona						
Pennsylvania (c)	1	2	33	1.000	1.000	
Massachusetts (c)	1	2	173	.954	.954	
Combined c					$\bar{x}$ = .977	
Pennsylvania (i)	3	2	403	.916 ± .074	.816 ± .106	0.721
B. selene						
Massachusetts (c)	7	10	1160	.960 ± .037	.896 ± .056	
Massachusetts (i)	5	2	692	.775 ± .118	.612 ± .068	1.525
South Dakota (i)	4	2	741	.830 ± .221	.685 ± .211	1.074
						$\bar{x}$ = 1.300
P. tharos						
Florida (c)	1	2	272	.864	.860	
Virginia (c)	4	4	1011	.990 ± .011	.988 ± .011	
West Virginia (c)	1	2	362	.983	.956	
Massachusetts (c)	1	2	648	1.000	.998	
Connecticut (c)	11	10	1606	.995 ± .006	.985 ± .024	
Combined c					$\bar{x}$ = .978	
Florida (i)	3	2	945	.941 ± .061	.635 ± .078	1.726
Texas (i)	2	2	137	.856 ± .144	.798 ± .174	0.813
West Virginia (i)	9	2	2412	.962 ± .048	.858 ± .081	0.525
						$\bar{x}$ = 1.021
P. pascoensis						
Montana (c)	5	8	945	.983 ± .028	.976 ± .027	
Alberta, Canada (c)	2	4	113	.965 ± .035	.965 ± .035	
Combined c					$\bar{x}$ = .973	
Montana (i)	2	2	305	.788 ± .181	.778 ± .192	0.895
Alberta, Canada (i)	3	2	751	.730 ± .146	.484 ± .016	2.793
						$\bar{x}$ = 1.844
P. campestris						
California (c)	2	4	562	1.000 ± .000	1.000 ± .000	
California (i)	1	2	406	.788	.749	1.404

Taxon / Locality			n			
T. batesii [1]						
New York (c)	5	8	2533	.938 ± .099	.929 ± .098	5.412
New York (i)	1	2	100	.950	.240	
J. coenia						
Florida (c)	1	2	208	1.000	1.000	0.130
Florida (i)	3	2	1373	.998 ± .002	.968 ± .026	
P. aegeria						
Hampshire, United Kingdom (c)	2	4	33	.931 ± .069	.931 ± .069	1.406
Hampshire, United Kingdom (i)	3	2	106	.655 ± .406	.655 ± .406	
P. megera						
Oxford, United Kingdom (c)	3	4	161	.973 ± .019	.938 ± .092	1.808
Boulogne, France (c)	2	4	146	.910 ± .025	.910 ± .025	1.715
Combined c				$\bar{x}$ = .927	$\bar{x}$ = .927	$\bar{x}$ = 1.762
Oxford, United Kingdom (i)	2	2	307	.870 ± .119	.590 ± .090	
Boulogne, France (i)	2	2	102	.938 ± .062	.604 ± .146	
P. rapae						
Pennsylvania (c)	3	6	334	.956 ± .008	.920 ± .010	1.070
Pennsylvania (i)	28	6	2186	.894 ± .105	.704 ± .151	
C. fulvicollis						
Connecticut (c)	7	14	546	.984 ± .030	.953 ± .054	2.394
Massachusetts (c)	1	2	171	1.000	.988	9.469
Texas (c)	1	2	223	.996	.991	2.610
Iowa (c)	6	12	1417	.985 ± .015	.963 ± .029	0.980
South Dakota (c)	6	12	367	.914 ± .091	.883 ± .090	0.508
Combined c				$\bar{x}$ = .939	$\bar{x}$ = .939	$\bar{x}$ = 3.192
Connecticut (i)	14	12	2185	.924 ± .057	.516 ± .253	
Massachusetts (i)	3	2	516	.975 ± .006	.088 ± .121	
Texas (i)	9	2	1673	.963 ± .047	.489 ± .148	
Iowa (i)	11	4	2415	.962 ± .027	.735 ± .179	
South Dakota (i)	1	2	248	.911	.827	
A. caja						
N.W. Germany (c)	5	?	4628	.936 ± .055	.888 ± .104	2.125
N.W. Germany (i)	11	?	10,587	.861 ± .159	.522 ± .287	

[1] Showing visible evidence of embryonic development.
[2] Mean ± standard deviation given if no. of broods >1.

Phyciodes t. tharos—FLORIDA: 4 mi. E of Cedar Key, Levy Co.; TEXAS: San Antonio, Bexar Co.; WEST VIRGINIA: Spruce Knob, elev 4500 ft, Pendleton Co.; PENNSYL-VANIA: Upper Tyrone Twp., Fayette Co.
P. t. pascoensis—MONTANA: 1 mi. S of Hall, Powell Co.; ALBERTA, CANADA: 6 mi. E of Nordegg, Red Deer.
P. campestris montana—CALIFORNIA: Lang Crossing, elev 4500 ft, S. Fork Yuba R., Nevada Co.
P. batesii—NEW YORK: Syracuse, Onondaga Co.
Junonia c. coenia—FLORIDA: Wauchula, Hardee Co.
Pararge aegeria tircis—ENGLAND: Pamber Forest, Hampshire.
P. m. megera—ENGLAND: Oxford, Oxfordshire; FRANCE: Boulogne-sur-Mer.
Pieris r. rapae—PENNSYLVANIA: Upper Tyrone Twp., Fayette Co.
Arctia c. caja—Northwest GERMANY.
Cisseps fulvicollis—CONNECTICUT: Woodbridge, New Haven Co.; MASSACHUSETTS: Littleton, Middlesex Co.; TEXAS: San Antonio, Bexar Co.; IOWA: Dubuque, Dubuque Co.; SOUTH DAKOTA: Custer Park, Custer Co.

Observations on embryonic survivorship included counts of eggs showing evidence of embryonic tissue differentiation (a darkening of egg color from pale yellow or green to brown or black) and of eggs hatching. An increase in failure to show embryonic development in the inbred broods was taken as evidence of very early embryonic mortality. There is a possibility that there was lowered fertilization rate of eggs in the inbred matings, but the males used in these matings were of the same age and condition as those used for laboratory control matings. Eggs from these control matings showed fertility equal to that from wild-fecundated females. Both visible fertility and incidence of egg hatch are combined under the term "hatchability."

The Wilcoxon Two-Sample Statistic (Owen, 1962) was used to compare differences in hatchability of broods in Part B. Calculations of load magnitude were made using the equations presented by Freire-Maia (1964), which are a simplification of those of Morton et al. (1956). Since the comparison is between inbred and control broods with $F = 0$, it is possible to use Freire-Maia's equation

$$B = \frac{\log(S_i/S_c)}{-0.4343F_i}$$

where B is the magnitude of the genetic load in lethal equivalents per zygote; S_i and S_c denote the mean survivorship of the inbred and control broods, respectively; and F_i is the coefficient of inbreeding of the inbred group. Morton et al. (1956), who used the term "mutant" to refer to any gene deleterious when homozygous, defined lethal equivalent (L. E.) as "a group of mutant genes of such number that if dispersed in different individuals, they would cause on the average one death, e.g., one lethal mutant, or two mutants each with a 50 per cent probability of causing death, etc."

Results

The results of Part A are shown in Table 1. In every species inbreeding caused a significant reduction in hatchability, but the amount varied greatly from one population and species to another. In the control broods hatching failure was due in the great majority of cases to infertility rather than to embryonic inviability. In the inbred broods, however, there were usually substantial reductions in both the incidence of visible embryonic development and in late embryonic viability. There was interspecific and interpopulation variation in the inbred broods in the proportion of mortality occurring before and after visible evidence of embryonic development. Variation in inviability was many times higher for the inbred broods than for the controls. The amount of variation was not a function of the magnitude of inbreeding depression. There were large differences between species and between populations in the size of the genetic load (L. E./zygote calculated from total hatchability) and of the standard deviation in viability observed for each series of broods.

The results of Part B are shown in Table 2. Hatchability within each family line of this population of *Phyciodes tharos* varied greatly, but only the family showing the least inbreeding depression (75-3) differed significantly (P < .005) from those showing the greatest (73-23, 73-31, 75-4).

Discussion

The degree of interbrood variation in hatchability (indicated by standard deviation) shown within each family line of *P. tharos* and the other Lepidoptera used here reveals that genetic loads in these species consist mainly of relatively few genetic units with strongly deleterious effects when homozygous. These genetic loads do not seem directly to reflect the genic variation that has been shown to occur in Lepidoptera.

Fig. 1 shows the distribution of L. E./zygote values for the 85 inbred *P. tharos* broods summarized in Table 2. The graph consists of four main peaks, with values clustered at or near 0, 1, 2, 3, and 4 L. E./ zygote. A distribution of this type could result from the action of only several strongly deleterious (i.e., lethal) recessive genes in each family, perhaps along with a few much weaker sublethals.

In Table 2 there is a considerable spread in L. E. values, even though only the very lowest value is significantly different from the highest. Thus, there is a spread on either side of the mean of about 0.7 L. E./zygote that is not significant here. If we assume for the

TABLE 2. Mean embryonic genetic loads expressed in F_1 progeny of sib-sib matings in 8 lines of *Phyciodes tharos* from Upper Tyrone Township, Pennsylvania.

Family line	No. of broods	No. of wild parents	No. of eggs	Hatched/laid[1]	L. E./zygote
controls	12	24	3037	.993 ± .011	
73-1	14	2	5884	.765 ± .154	1.043
73-4	9	2	2459	.803 ± .184	0.850
73-23	9	4	2663	.596 ± .272	2.041
73-31	9	4	2595	.591 ± .146	2.076
75-1	12	2	3749	.779 ± .132	0.971
75-2	11	2	3046	.683 ± .172	1.494
75-3	12	2	3021	.888 ± .113	0.448
75-4	9	2	2571	.671 ± .190	1.623
					$\bar{x} = 1.318$

[1] Mean ± standard deviation.

moment that this amount of variation applies also to the other species in Table 1, all except *P. batesii, J. coenia,* and *C. fulvicollis* probably fall within the normal range of *P. tharos* and form a fairly homogeneous group. The single value for *P. batesii* falls at the upper limit of values for *P. tharos* (above 98.81% of values in Fig. 1), but this single sample cannot be considered significant. All three values of *J. coenia* are at the lower level for *P. tharos;* there is a less than .001 chance of any three randomly picked values of *P. tharos* from Fig. 1 all falling this far to one end of the graph. The overall mean L. E./zygote value for *C. fulvicollis* falls at the upper end of the graph. From this it seems likely that *C. fulvicollis* and at least this population of *J. coenia* carry genetic loads that are, respectively, larger and smaller than those of the other species. A very small genetic load would seem adaptive for the inbred populations resulting from the sort of colonization events that occur in *J. coenia.* Too little is known about the population structure of *C. fulvicollis* to speculate on the comparatively large genetic load it carries.

The lethal equivalent values calculated here are generally in line with those estimated for other insects. One to two L. E./zygote have been estimated (by survival from egg to adult) for *Drosophila* (Diptera) (Dobzhansky et al., 1963; Stone et al., 1963; Malogolowkin-Cohen et al., 1964) and for *Tribolium* (Coleoptera) (Levene et al., 1965). For humans a value of 3 to 5 L. E./zygote (by survival from birth to sexual maturity) has been established by Morton et al. (1956), whereas embryonic loads in Douglas-fir average about 10 L. E./zygote (Sorenson, 1969). In none of these organisms has a definite relationship been shown between magnitude of load and population structure. The general similarity of load magnitude among the very different
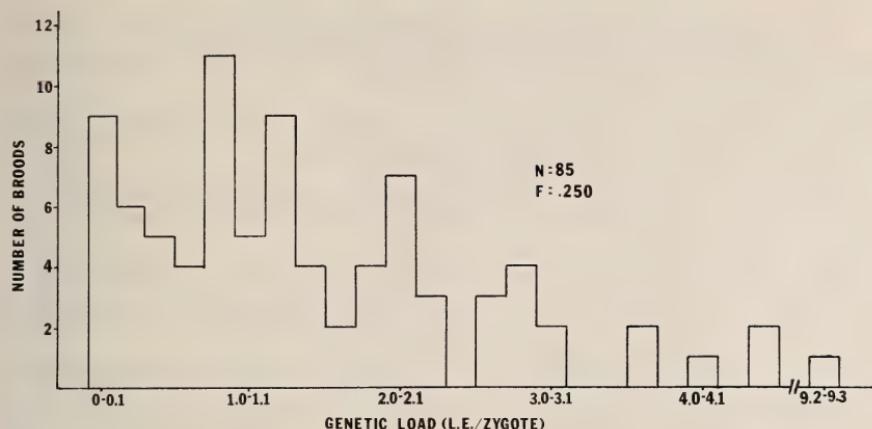
FIG. 1. Distribution of embryonic genetic loads in lethal equivalents per zygote in 85 inbred broods of *Phyciodes tharos* from Upper Tyrone Township, Pennsylvania.

insects thus far examined may indicate that genetic loads are more related to some internal genetic balancing responsible for the metabolic integration of the individual organism than to population structure. However, there are surely situations (as in species colonizing by single fecundated females) where adjustment of load magnitude is highly adaptive.

LITERATURE CITED

BURNS, J. M. & F. M. JOHNSON. 1967. Esterase polymorphism in natural populations of a sulfur butterfly, *Colias eurytheme*. Science 156: 93–96.

DOBZHANSKY, TH. 1970. Genetics of the Evolutionary Process. Columbia Univ. Press, New York. 505 pp.

———, B. SPASSKY, & T. TIDWELL. 1963. Genetics of natural populations. XXXII. Inbreeding and the mutational and balanced genetic loads in natural populations of *Drosophila pseudoobscura*. Genetics 48: 361–373.

FREIRE-MAIA, N. 1964. Estimate of the genetic load disclosed by inbreeding. Genetics 50: 527–529.

KOSUDA, K. 1972. Synergistic effect of inbreeding on viability in *Drosophila virilis*. Genetics 72: 461–468.

LEVENE, H., I. M. LERNER, A. SOKOLOFF, F. K. HO & I. R. FRANKLIN. 1965. Genetic load in *Tribolium*. Proc. Natl. Acad. Sci. (U.S.A.) 53: 1042–1050.

LEWONTIN, R. C. 1974. The Genetic Basis of Evolutionary Change. Columbia Univ. Press, New York. 346 pp.

MALOGOLOWKIN-COHEN, CH., H. LEVENE, N. P. DOBZHANSKY & A. SOLIMA-SIMMONS. 1964. Inbreeding and the mutational and balanced loads in natural populations of *Drosophila willistoni*. Genetics 50: 1299–1311.

MORTON, N. E., J. F. CROW & H. J. MULLER. 1956. An estimate of the mutational damage in man from data on consanguineous marriages. Proc. Natl. Acad. Sci. (U.S.A.) 42: 855–863.

OLIVER, C. G. 1972a. Genetic and phenotypic differentiation and geographic distance in four species of Lepidoptera. Evolution 26: 221–241.

——— 1972b. Genetic differentiation between English and French populations of the satyrid butterfly *Pararge megera*. Heredity 29: 307–313.

——— 1977. Genetic incompatibility between populations of the nymphalid butterfly *Boloria selene* from England and the United States. Heredity 39: 279–285.

——— 1978. Experimental hybridization between the nymphalid butterflies *Phyciodes tharos* and *P. campestris montana*. Evolution 32: 594–601.

——— 1979. Experimental hybridization between *Phyciodes tharos* and *P. batesii* (Nymphalidae). J. Lepid. Soc. 33: 6–20.

OWEN, D. B. 1962. Handbook of Statistical Tables. Addison-Wesley, Reading, Mass. 580 pp.

PISANI, J. F. & W. E. KERR. 1961. Lethal equivalents in domestic animals. Genetics 46: 773–786.

RICHMOND, R. C. 1972. Enzyme variability in the *Drosophila willistoni* group. III. Amounts of variability in the superspecies *D. paulistorum*. Genetics 70: 87–112.

SHAPIRO, A. M. 1978. A new weedy host for the buckeye, *Precis coenia* (Nymphalidae). J. Lepid. Soc. 32: 224.

SITTMANN, K., H. ABPLANALP & R. A. FRASER. 1966. Inbreeding depression in Japanese quail. Genetics 54: 371–379.

SORENSON, F. 1969. Embryonic genetic load in coastal Douglas-fir, *Pseudotsuga menziesii* var. *menziesii*. Amer. Natur. 103: 389–398.

STONE, W. S., F. D. WILSON & V. L. GERSTENBERG. 1963. Genetic studies of natural populations of *Drosophila: Drosophila pseudoobscura*, a large dominant population. Genetics 48: 1089–1106.

VAWTER, A. T. & P. F. BRUSSARD. 1975. Genetic stability of populations of *Phyciodes tharos* (Nymphalidae: Melitaeinae). J. Lepid. Soc. 29: 15–23.

DESCRIPTION OF THE LARVA OF *PHALAENOPHANA EXTREMALIS* WITH NOTES ON *P. PYRAMUSALIS* (NOCTUIDAE)

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ABSTRACT. The mature larva of *Phalaenophana extremalis* (Barnes & McDunnough) (Noctuidae) is described and illustrated. The phylogenetic relationships of *P. extremalis* and *P. pyramusalis* (Walker) are discussed.

The noctuid genus *Phalaenophana* Grote (Herminiinae) is a small taxon containing but two North American species (McDunnough, 1938) and two in South America (Forbes, 1954). The Nearctic species are *P. pyramusalis* (Walker) and *P. extremalis* (Barnes & McDunnough). Walker (1859) simply listed the type-locality of the former species as "United States," and Grote (1873) described the same species under *rurigena* from Hastings, New York and Pennsylvania. Later authors have described the distribution for *P. pyramusalis* to include the area extending from Nova Scotia to Florida and westward to Saskatchewan and Texas (Forbes, 1954; Kimball, 1965). The mature larva of *P. pyramusalis* was described from Tennessee specimens that fed on "... forest leaves black with decay" (Crumb, 1934, 1956). Forbes (1954) listed its larval food as wilted and dry leaves. The type-locality of the moth of *P. extremalis* is the "White Mts., Ariz." (Barnes & McDunnough, 1912). Other known collecting localities for this species are the Huachuca Mountains, Arizona and Beulah, New Mexico (unpublished records, United States National Museum of Natural History (USNMNH)). The larva of *P. extremalis* is unknown.

This paper describes the mature larvae of *P. extremalis* reared from the Chiricahua Mountains, Cochise Co., Arizona, and comments on its phylogenetic status. All techniques, morphological terminology, and abbreviations used in this study were reported previously (Godfrey, 1972). The specimens examined are from the collection of John G. Franclemont.

Phalaenophana extremalis (Barnes & McDunnough)

General. Head width 1.28–1.40 mm. Total head and body length 12.7–13.3 mm (inflated) (one uninflated, recently moulted specimen measured 9.2 mm). Metathoracic coxae contiguous to narrowly separated. Prolegs present on Ab3–6, 10, size increasing caudad on Ab3–6, those on Ab3 about ½ size of those on Ab6 (Fig. 1). Crochets homoideous, uniordinal. Integument of head and body granulated. Head granules at 100× small, beaded. Body granules at 100× heterogeneous (except on cervical shield as noted below), conical, bearing minute ridges that converge distad, some granules quite coarse. Dorsal setae on Ab1–8 (Fig. 8) arising from conspicuous, broad based, conical
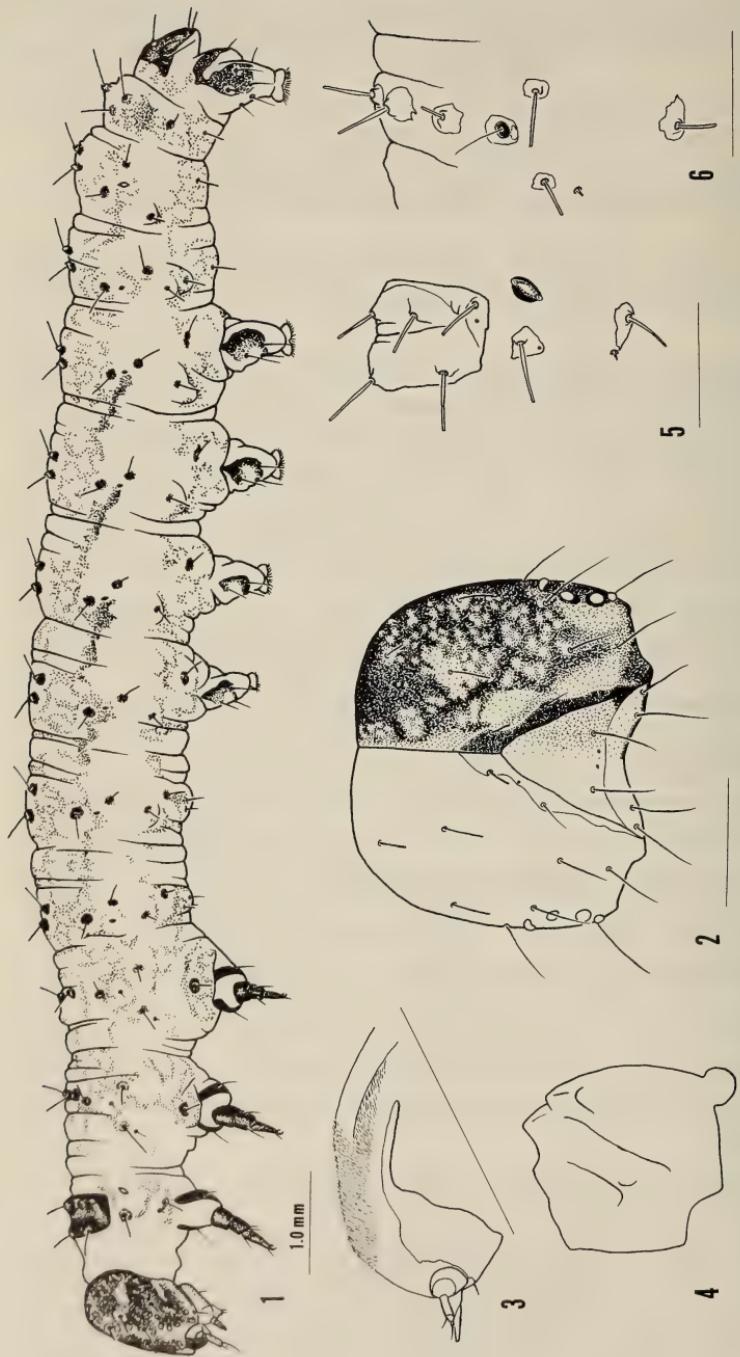
FIGS. 1–6. *Phalaenophana extremalis* larva: **1**, lateral habitus; **2**, frontal view of head; **3**, lateral view of hypopharyngeal complex; **4**, oral aspect of left mandible; **5**, left dorsolateral setal arrangement of prothorax; **6**, left dorsolateral setal arrangement of mesothorax. Scale lines = 0.5 mm except as noted.

tubercles; setae D1 projecting cephalad, D2 caudad; setae with blunt tips, distal ⅓ of setae appearing slightly constricted. Spiracles weakly emarginate.

Head (Fig. 2). Postgenal sutures slightly sigmoid but not converging distad. Length of epicranial suture 0.54–0.62 mm. Height of frons 0.42–0.50 mm. Distance from F1 to anterior edge of clypeus 0.13–0.16 mm. Interspace F1–F1 0.24 mm. AF2 posterior of frons apex. Setae A1–3 forming obtuse angle at A2. Interspace P1–P1 slightly less than subequal to P2–P2. Distance from P1 to epicranial suture about ⅓ P1–L. Transverse line through P1 passing posterior of juncture of adfrontal ecdysial line and on or slightly posterior of L setae. Setae AF2, L, P1–2 blunt distally. Remaining head setae tapering distad. P2 setigerous tubercle, when viewed laterally, slightly raised and projecting cephalad. Ocellar spacing: Oc1–Oc2 0.05–0.06 mm, Oc2–Oc3 0.04–0.05 mm, Oc3–Oc4 0.03 mm.

Mouthparts. Hypopharyngeal complex (Fig. 3): spinneret tapering distad; stipular seta about ⅓ Lpsl, subequal to Lp1; Lp1 greater than Lps2; slightly less than Lp2; tip of Lp2 approximating distal lip of spinneret; distal ¼ of hypopharynx above spinneret barren of spines, remainder of distal and proximolateral regions clothed with numerous, short, thin spines. Mandible (Fig. 4): lateral surface bearing two setae; inner surface with two ridges not extending to tips of outer teeth; outer teeth 1–4 triangular, the 4th rather low and reduced.

Thorax. Segment T1 (Fig. 5): cervical shield distinctly sclerotized, covered with small, homogeneously-sized, beaded granules similar to those on head; distinct transverse depression between XD and D tubercles; depression behind D2 tubercles extends ventrad then curves cephalad before terminating anterior of SD tubercles; shield includes SD tubercles; SD1 and L2 setigerous tubercles visible at 100× but their setae are absent; all setae except V's and those on legs bluntly tipped. Tubercles of SV contiguous to narrowly separated. Spiracle transversely aligned with posterior margin of cervical shield. Segments T2–3 (Fig. 6): SD1 thin, hairlike; setae D–SV bluntly tipped. Tarsal setae (Fig. 7): Ts1 slightly lanceolate; Ts2 narrow, tapering distad; Ts3 spatulate; Ts4 narrow, tapering distad.

Abdomen. Ab1–6 with 3 SV setae, Ab7–9 with 1 each. Ab1–6 lateral chaetotaxy as shown in Fig. 1. Ab9: D1 and SD1 setae subequal; tubercles D1 and SD1 separated from each other (Fig. 9). Subanal setae on Ab10 widely spaced (Fig. 10). Length of D1's on Ab6–7 0.19–0.24 mm, D2's 0.24–0.28 mm. Height of Asp7 0.08–0.09 mm, Asp8 0.12–0.16 mm.

Coloration (preserved material). Head with dark brown coronal stripes and reticulation (Fig. 2). Body pale with contrasting, broad, brown middorsal stripe extending from T2 through Ab10, especially intensified on anterior half of each segment. Middorsal line on cervical shield pale. Tubercles, thoracic legs, and lateral shields of prolegs dark brown. Ab1–6 with brown oblique stripes starting in front of spiracle and extending dorsocephalad (Fig. 1), dorsal margin of lateral area appearing dentate.

Material examined. Five specimens: "Upper Campground," Pinery Canyon, elev. 7000 ft, Chiricahua Mountains, Cochise Co., Arizona. Reared August–December 1967 on dead oak leaves (*Quercus* spp.) by G. L. Godfrey. Reared from eggs of associated female moth determined by J. G. Franclemont.

Remarks. The generic description for the larva of *Phalaenophana* that Crumb (1934) proposed is based on *P. pyramusalis*. Although his description is quite detailed, he emphasized two sets of characters; namely, the positions of the head setae P1 and P2 relative to each other, seta L, and the epicranial suture and the nature of the subanal setae, to separate *Phalaenophana* from many other herminiine genera. The conditions in *P. pyramusalis* are P1–P1 slightly less than P2–P2 and P1 distinctly closer to the epicranial suture than to L; the subanal setae are approximate and form an anal fork (Fig. 11). The only slight modification of the cephalic chaetotaxy in *P. extremalis* is that P1–P1 and P2–P2 may attain subequality. The structure of the latter species' subanal setae (Fig. 10) deviates strikingly from the generic description. The setae are widely spaced and too small to be called an anal fork.

The hypopharyngeal complexes of the two species are similar, the only difference being that the spinneret of *P. extremalis* is slightly longer than that of *P. pyramusalis*.
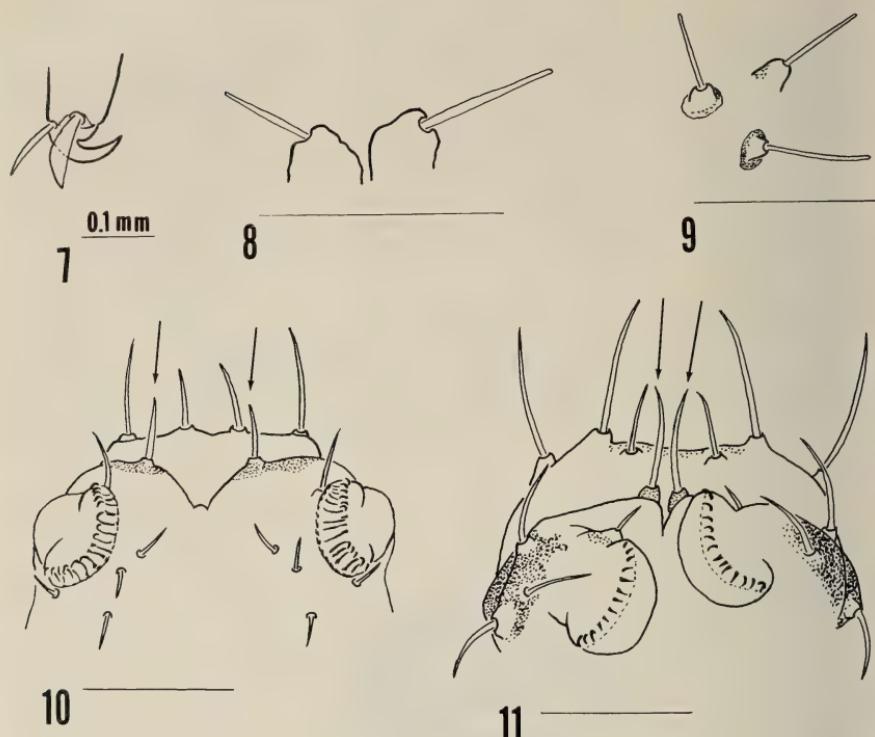
FIGS. 7–11. *Phalaenophana extremalis:* **7,** posterior view of tarsal setae; **8,** setae D1–2 on Ab7; **9,** setae D1–2 and SD1 on Ab9; **10,** ventral view of Ab10 showing subanal setae. *P. pyramusalis:* **11,** ventral view of Ab10 showing subanal setae. Scale lines = 0.5 mm except as noted.

The inner mandibular surface of *P. extremalis* lacks any suggestion of an inner tooth on the first inner ridge. A tooth is present in *P. pyramusalis*, albeit small. Series of newly moulted and older *P. extremalis* ultimate instar larvae need to be examined and compared to determine if the absence of the inner tooth is a specific characteristic or whether the absence is the result of mandibular wear.

The nature of the SD and L setae on T1 may be a useful generic character that was not considered by Crumb except in reference to the extent of which the cervical shield includes the SD setal bases. On the mature larva of *P. extremalis*, SD1 and L2 of T1 occur only as vestigial setigerous tubercles; the actual setae are absent (Fig. 5). These tubercles and setae are present on T1 in *P. pyramusalis*. As a side note, both SD1 and L2 prothoracic tubercles and setae are absent in the herminiine genus *Renia* (Godfrey, 1980).

I have some reservations about whether *P. extremalis* and *P. pyramusalis* are in fact congeneric, based on the differences of the subanal setae and SD1 and L2 on the prothoracic segment of the two species. However, I am hesitant to suggest with which genus *extremalis* might be more naturally grouped, because my knowledge of the larval Herminiinae as a whole is yet limited. It becomes increasingly apparent that the generic limits of the herminiines need to be redefined following an overall assessment of new characters and reconsideration of old ones.

ACKNOWLEDGMENTS

LITERATURE CITED

BARNES, W. & J. H. McDUNNOUGH. 1912. Fifty new species. Contrib. Nat. Hist. Lepid. North Amer. 1(5): 3–36.

CRUMB, S. E. 1934. A classification of some noctuid larvae of the subfamily Hypeninae. Entomol. Amer. 14 (N.S.): 133–197.

——— 1956. The larvae of the Phalaenidae. U.S. Dept. Agr. Tech. Bull. 1135. 356 pp.

FORBES, W. T. M. 1954. Lepidoptera of New York and neighboring states. Pt. 3. Cornell Univ. Agr. Exp. Sta. Mem. 329. 433 pp.

GODFREY, G. L. 1972. A review and reclassification of larvae of the subfamily Hadeninae (Lepidoptera, Noctuidae) of America north of Mexico. U.S. Dept. Agr. Tech. Bull. 1450. 265 pp.

——— 1980. Larval descriptions of *Renia hutsoni*, *R. rigida* and *R. mortualis* with a key to larvae of *Renia* (Lepidoptera: Noctuidae). Proc. Entomol. Soc. Washington, 82(3): 457–468.

GROTE, A. R. 1873. Descriptions of North American Noctuidae.—No. 3. Trans. Amer. Entomol. Soc. 4: 293–310.

KIMBALL, C. P. 1965. Arthropods of Florida and neighboring land areas, I: Lepidoptera of Florida, an annotated checklist. 363 pp. Gainesville, Fla.

McDUNNOUGH, J. 1938. Check list of the Lepidoptera of Canada and the United States of America. Pt. 1, Macrolepidoptera. S. Calif. Acad. Sci. Mem. 1(1): 1–275.

WALKER, F. 1858[1859]. List of the specimens of lepidopterous insects in the collection of the British Museum. Pt. 16—Deltoides. London. 253 pp.

THE MONTANE BUTTERFLY FAUNA OF THE
SPRING RANGE, NEVADA

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ABSTRACT. The butterflies of the Spring Range in southern Nevada show complex biogeographical relationships and several features of an insular fauna. The range is at the southern end of a series of north-south mountain ranges of the Great Basin, is the highest in the Mojave Desert and is near the boundary of the hot southern and cool northern deserts. Five of its 80 butterfly taxa are endemic; the remaining taxa show affinities towards the Great Basin and Rocky Mountains among the truly montane species. There is also considerable impoverishment not only in total species number when compared to areas of the Sierra Nevada and Rocky Mountains but also in number of montane species.

The Spring Range in southern (Clark Co.) Nevada is of considerable biogeographic interest. It marks the southern terminus of the high elevation series of Great Basin mountain masses, is geographically isolated from other ranges of similar mass and elevation by some 80 mi of mostly low elevation desert, is the highest elevation range in the Mojave Desert and is located near the blend zone of the hot Mojave and cool Great Basin deserts. The Spring Range is relatively well known biologically with major works published on its plants and zonation of vegetation (Clokey, 1951; Bradley & Deacon, 1965, Beatley 1976), birds (van Rossem, 1936; Johnson, 1965) and mammals (Hall, 1946). There is no formal account of its butterfly fauna although the range has been visited by numerous collectors since at least the 1920's (Garth, 1928). The butterflies of the range are now sufficiently well known for analysis.

This paper presents a list of the butterfly fauna of the Spring Range, examines its affinities and discusses the montane species in relation to the insular nature of the area. Throughout, a montane species is one which is restricted to the higher elevations and is not (or very rarely) resident in the desert valleys. A more detailed account of the entire Clark Co. butterfly fauna will be published separately.

Description of Area

The Spring Range rises from the valley floor at about 2000 ft to an elevation of 11,910 ft at Charleston Peak. The vegetation at the lower elevations to about 6000 ft is desert scrub dominated by creosote bush (*Larrea tridentata*) and burrobush (*Ambrosia dumosa*) on the lower slopes and blackbush (*Coleogyne ramosissima*) on the higher bajadas. Between 6000 and 7500 ft is a woodland dominated by Piñon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*). Above this is for-

est dominated by ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*) at lower elevations and limber and bristlecone pines (*Pinus flexilis* and *P. aristada*) at the higher elevations. On the higher ridges are areas of dry meadow. There are few openings in the forest except for areas cleared by man (e.g., Lee Canyon ski area, the old ski run in Kyle Canyon), a small dry meadow in Lee Canyon, and areas disturbed by fire or snow slides. Permanent and semi-permanent water are limited to such areas as upper Kyle Canyon, Deer Creek Canyon and in the Willow and Cold creeks area. In certain areas, especially on the southeast slope, the zonation of vegetation is considerably depressed in cool canyons.

The Fauna

Eighty species of butterflies have been recorded above 6000 ft in the Spring Range of which at least 56 are resident. Thirty-two of these are considered montane taxa (Tables 1, 2). The total number of species compares favorably with other Great Basin mountain ranges (Table 3) especially considering that the latter have not been studied as intensively, for the most part, as the Spring Range. The total falls far short of those for areas within the Rocky Mountain or Sierra Nevada systems.

Endemism

Five subspecies of butterflies are endemic (or nearly so) to the Spring Range. All are quite distinctive. *Speyeria zerene carolae* (considered by some to be a *S. coronis* (Behr) subspecies; authors of Spring Range taxa given in Tables 1, 2) appears to have no close relatives. *Euphydryas anicia morandi* likewise has no apparent close relationship to other *anicia* populations. *Limenitis weidemeyerii nevadae* also occurs in the nearby Sheep Range and probably evolved from an isolate of the narrow-banded southern Rocky Mountain population, *L. w. angustifascia* (Barnes & McDunnough). No intermediate populations have been found although *L. w. angustifascia* and the Great Basin population *L. w. latifascia* Perkins & Perkins appear to blend widely in southern Utah and eastern Nevada. The recently described (Austin, 1980) *Plebejus shasta charlestonensis* is the most distinct of the *shasta* subspecies and is probably allied more closely with the Great Basin populations of *P. s. minnehaha* (Scudder) than with nominate *shasta* (Edwards) of the Sierras. Relationships of the undescribed *Euphilotes enoptes* (Boisduval) population are unclear and require further study.

Certain other Spring Range populations (e.g., *Papilio rutulus, Plebejus icarioides evius, Coenonympha ochracea brenda* are somewhat

Table 1. The resident butterfly fauna (above 6000 ft) of the Spring Range, Nevada and its relationship to other montane areas.

Spring Range Taxon	Sierra Nevada	Great Basin	Rocky Mountain	Biogeographical Affinity[1]
Hesperia comma harpalus (Edwards)*[2]	yosemite[3]	X[4]	susanae +[5]	GB
Hesperia nevada (Scudder)*	X	X	X	WNA
Hesperia juba (Scudder)*	X	X	X	WNA
Pholisora alpheus oricus Edwards	—	X	alpheus	GB
Heliopetes ericetorum (Boisduval)	(L)[6]	(L)	X	WNA
Pyrgus scriptura (Boisduval)	X	—	X	WNA
Pyrgus communis (Grote)	X	X	X	WS
Erynnis brizo burgessi (Boisduval & Le Conte)*	—	—	(L)	RM
Erynnis meridianus meridianus (Bell)*	—	—	X	SWD
Papilio bairdii Edwards*	X	X	X	WNA
Papilio rutulus Lucas*	X	X	X	WNA
Neophasia menapia menapia (Felder & Felder)*	tau	X	X	RM
Pieris beckerii beckerii Edwards	X	X	X	WNA
Pieris sisymbrii elivata (Barnes & Benjamin)*	sisymbrii	X	X	RM
Pieris protodice protodice Boisduval & Le Conte	X	X	X	WS
Pieris rapae (Linnaeus)	X	X	X	WS
Colias eurytheme eurytheme Boisduval	X	X	X	WS
Anthocaris sara thoosa Scudder*	sara+	X+	julia	MD
Euchloe hyantis lotta (Beutenmuller)	hyantis	X	X	RM
Apodemia mormo mormo (Felder & Felder)	(L)+	X	(L)+	GB
Satyrium behrii behrii (Edwards)*	X	crossi	crossi	SN
Callophrys fotis fotis (Strecker)*	windi	X	C. mossi	GB
Callophrys spinetorum (Hewitson)*	X	X	X	WNA
Callophrys siva siva (Edwards)*	—	undes. ssp.	X	RM
Callophrys sheridanii comstocki Henne	lemberti	neoperplexa	sheridanii	MD
Atlides halesus corcorani Gunder	(L)	(L)	(L)	SWD
Strymon melinus pudica (Edwards)	X	X+	franki	SWD
Brephidium exilis (Boisduval)	(L)	(L)	(L)	T

	(L)	(L)	(L)	T
Leptotes marina (Reakirt)				SWD
Hemiargus ceraunus gyas (Edwards)			—	WS
Hemiargus isola alce (Edwards)		(L)	X	SCM
Plebejus icarioides evius (Boisduval)*	icarioides+	ardea	lycea+	E
Plebejus shasta charlestonensis Austin*	shasta	minnehaha	pitkinensis	SWD
Plebejus acmon texanus Goodpasture	acmon	(L)+	lutzi	WNA
Everes amyntula (Boisduval)*	X	X	X	E
Euphilotes enoptes (Boisduval) ssp.*	enoptes	ancilla	ancilla	RM
Glaucopsyche lygdamus oro Scudder*	incognitus		X	RM
Celastrina argiolus cinerea (Edwards)*	echo	echo	X	E
Limenitis weidemeyerii nevadae (Barnes & Benjamin)*	latifascia(L)	latifascia	angustifascia+	SWD
Adelpha bredowii eulalia (Doubleday)*	californica	(L)	X	WS
Vanessa atalanta rubria (Fruhstorfer)	X	X	X	WS
Vanessa virginiensis (Drury)	X	X	X	WS
Vanessa cardui (Linnaeus)	X	X	X	WNA
Vanessa annabella (Field)	X	X	X	WNA
Nymphalis californica (Boisduval)*	X	X	X	WNA
Nymphalis milberti furcillata (Say)*	X	X	X	WS
Nymphalis antiopa antiopa (Linnaeus)	X	X	X	WS
Polygonia satyrus (Edwards)	X	X	X	WNA
Polygonia zephyrus (Edwards)*	X	X	X	
Chlosyne palla vallismortis (Johnson)*	whitneyi+	—	flavula+	MD
Thessalia leanira alma (Strecker)*	—	X	T. fulvia	GB
Poladryas minuta arachne (Edwards)*	monache	(L)	X	RM
Euphydryas anicia morandi Gunder*	—	wheeleri+	eurytion+	E
Speyeria zerene carolae dos Passos & Grey*	zerene+	platina+	cynna	E
Coenonympha ochracea brenda Edwards*	C. ampelos		ochracea	GB
Cercyonis sthenele (Boisduval) ssp.*	silvestris	paulus	masoni	MD

[1] GB = Great Basin, WNA = Western North America, WS = Widespread, RM = Rocky Mountain, SWD = Southwest Deserts, MD = Mojave Desert, SN = Sierra Nevada, T = Tropical, SCM = Southern California Mediterranean, E = Endemic.

[2] * = montane taxon.

[3] Names refer to other subspecies or closely related species that are present in the fauna.

[4] X = same taxon present as in the Spring Range.

[5] + = another, less widespread, subspecies of the species is also present in the fauna.

[6] (L) = occurs very locally in this fauna or occurs marginally with center of distribution in another fauna.

TABLE 2. Non-resident butterfly species occurring at the higher elevations (above 6000 ft) of the Spring Range, Nevada.

Megathymus yuccae navajo Skinner	*Phoebis sennae marcellina* (Cramer)
Lerodea eufala (Edwards)	*Eurema nicippe* (Cramer)
Ochlodes yuma (Edwards)	*Nathalis iole* Boisduval
Polites draco (Edwards)	*Ministrymon leda* (Edwards)
Hylephila phyleus (Drury)	*Lycaena dorcas castro* (Reakirt)
Copaeodes aurantiaca (Hewitson)	*Libytheana bachmanii larvata* (Strecker)
Pholisora libya libya (Scudder)	*Precis coenia* (Hubner)
Thorybes pylades (Scudder)	*Chlosyne californica* (Wright)
Battus philenor philenor (Linnaeus)	*Phyciodes mylitta mylitta* (Edwards)
Papilio rudkini Comstock	*Danaus plexippus plexippus* (Linnaeus)
Papilio indra martini Emmel & Emmel	*Danaus gilippus strigosus* (Bates)
Colias cesonia (Stoll)	*Coenonympha california california* Westwood

divergent from other populations but may not be distinctive enough to warrant formal taxonomic recognition. The population of *Chlosyne palla* (Boisduval) also deserves mention here. It appears very close to *C. p. vallismortis* known elsewhere only from the Panamint Mountains in the Death Valley region of California, some 80 mi W of the Spring Range.

The butterflies of the Spring Range thus show one feature of insularity, endemism. Of the resident taxa, 8.9% are endemic. This level of endemism appears unparalleled elsewhere in the Great Basin and places the Spring Range in a class that few other continental areas can rival. Endemism in the Spring Range is also known for other groups. Plants exhibit about 5% endemism at the higher elevations (Clokey, 1951) and 2 of 34 mammals are endemic (5.9%, Hall, 1946). Endemism among plants is greater in the Spring Range than in any other range studied in the Great Basin (Harper et al., 1978). Four subspecies of birds described from the Spring Range were once thought to be endemic. Three of these, however, are not distinct enough to warrant taxonomic recognition and the other is more widespread than previously thought (Johnson, 1965; Austin & Rea, 1976).

Impoverishment

Another feature of insular biotas is impoverishment. As mentioned above, the Spring Range has a representative number of taxa as compared with other Great Basin ranges but far fewer than areas in the Sierra Nevada or Rocky Mountains. The number of species of other groups (i.e., vascular plants, Harper et al., 1978; boreal mammals and birds, Brown, 1978) is also lower than in either of the main western

TABLE 3. Comparison of the Spring Range, Nevada butterfly fauna with those of other western montane areas.

Locality	Number of species	Number of montane species
Sierra Nevada		
Lake Tahoe area[1]	96	57
Donner Pass[2]	83	57
Yosemite[3]	134	82
Great Basin		
Toiyabe Range, Nevada[4]	77	42
Jarbidge Mts., Nevada[4]	73	44
Snake Range, Nevada[4]	74	43
Stansbury Mts., Utah[5]	69	37
Spring Range, Nevada[6]	80	32
Rocky Mountains		
Wasatch-Unitah area, Utah[5]	119	80
Clear Creek Co., Colorado[7]	124	74

[1] Nevada State Museum, D. Bauer and personal records.
[2] Emmel & Emmel, 1962, 1974.
[3] Garth & Tilden, 1963.
[4] Nevada State Museum and personal records.
[5] Tidwell & Callaghan, 1972.
[6] This study.
[7] Brown et al., 1957.

ranges and about intermediate among several Great Basin ranges that have been studied. The impoverishment among butterflies is particularly striking when montane species are considered (Table 3). The Spring Range is inhabited by far fewer montane species than not only the Rockies and Sierras but also the various ranges of the Great Basin.

This impoverishment results from a poor representation of large genera and the absence of certain widespread montane species. The Spring Range has but one *Speyeria*, a *zerene* subspecies. Most other western ranges have in addition at least representatives of *coronis*, *callippe* (Boisduval) and *egleis* (Behr). The genus *Phyciodes* is absent (only 2 records of *mylitta*). Coppers are also absent from the Spring Basin except for one old record of *L. dorcas*. Other Great Basin ranges often have *L. arota* (Boisduval), *L. nivalis* (Boisduval) and *L. heteronea* Boisduval. Other widespread montane taxa which are absent from the Spring Range include *Papilio zelicaon* Lucas, *P. multicaudatus* Kirby, *Euchloe ausonides* Lucas, *Chlosyne acastus* (Edwards), *Euphydryas editha* (Boisduval), *Callophrys eryphon* (Boisduval), *Plebejus saepiolus* (Boisduval) and *Glaucopsyche piasus* (Boisduval).

Impoverishment probably is due to several mechanisms. Extinction may play a role (as is possible with *Lycaena dorcas* cited above). Distance from source populations also may be important. The few records of such species as *Coenonympha california* (one record), *Phy-*

ciodes mylitta (two records), *Lycaena dorcas* (one record) and *Thorybes pylades* (two records) suggest that occasional individuals of non-resident species reach the Spring Range as strays (windblown?) but are incapable of establishing themselves because of factors such as low population density, lack of mates and/or low density or absence of suitable foodplants.

The major cause of impoverishment among Spring Range butterflies is undoubtedly related to low habitat diversity as was suggested for birds (Johnson, 1975). Habitat diversity, according to Johnson's (1975) concept takes into account the number of conifer species, extent of riparian vegetation and extent of permanent water. The Spring Range falls toward the lower end in habitat diversity (Johnson, 1975), containing few species of conifers and little permanent water or riparian vegetation. There is also no true development of alpine vegetation on the higher ridges. This poor representation of certain habitats (and their associated plants) has undoubtedly led to the extinction of and/or prevented the establishment of species characteristic of such habitats.

Biogeography

Each resident taxon occurring in the Spring Range was assigned to a biogeographic element based on its distribution (Table 1). Also, in this table, the relationships to other faunas are presented. Where the Spring Range taxon does not occur, the most closely related taxon is named (if one is present). In some areas, more than one closely related subspecies occurs in another fauna. The most widespread is identified and the presence of another is indicated.

Over 40% of the Spring Range butterflies have wide distributions in western North America or beyond (Table 4). Of the remaining taxa, nearly one-third have hot desert affinities either throughout the region or more locally and include both lowland and montane elements. An additional eight taxa have Rocky Mountain affinities and six have primarily Great Basin relationships. Only one taxon is related to the Sierra Nevada fauna.

When the montane species alone are considered, only 28% are widespread (all are western species), 22% are Rocky Mountain, 16% are endemic and 13% are Great Basin. The desert element is considerably less important comprising only 22% of the non-widespread taxa. Other groups of biota show similar relationships. Nearly one-half of the plants are of Great Basin origin (Clokey, 1951). Birds show both Rocky Mountain and Great Basin affinities with almost no Sierra Nevada influence (Johnson, 1965).

TABLE 4. Biogeographic relationships of the resident butterfly fauna (above 6000 ft) of the Spring Range, Nevada.

Biogeographical element	Total fauna (%)	Montane fauna (%)
Widespread	17.9	0.0
Western North America	23.2	28.1
Tropical	3.6	0.0
So. California Mediterranean	1.8	3.1
Southwestern Desert	10.7	6.3
Mojave Desert	7.1	9.4
Great Basin	10.7	12.5
Rocky Mountain	14.3	21.9
Sierra Nevada	1.8	3.1
Endemic	8.9	15.6
Number of species	56	32

LITERATURE CITED

AUSTIN, G. T. 1980. A new *Plebejus* (*Icaricia*) *shasta* (Edwards) from southern Nevada (Lycaenidae). J. Lepid. Soc. 34: 20–24.

———— & A. M. REA. 1976. Recent southern Nevada bird records. Condor 78: 405–408.

BEATLEY, J. C. 1976. Vascular plants of the Nevada Test Site and central-southern Nevada: ecological and geographical distributions. Natl. Tech. Info. Center, Springfield, Virginia.

BRADLEY, W. G. & J. E. DEACON. 1965. The biotic communities of southern Nevada. Nev. State Mus. Anthro. Papers, no. 13, pt. 4: 201–295.

BROWN, F. M., D. EFF & B. ROTGER. 1957. Colorado butterflies. Denver Mus. Nat. History, Denver, Colorado.

BROWN, J. H. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. Great Basin Nat. Mem. 2: 209–227.

CLOKEY, I. W. 1951. Flora of the Charleston Mountains, Clark County, Nevada. Univ. Calif. Publ. Botany 24: 1–274.

EMMEL, J. F. & T. C. EMMEL. 1974. Ecological studies of Rhopalocera in a Sierra Nevada community—Donner Pass, California. V. Faunal additions and foodplant records since 1962. J. Lepid. Soc. 28: 347–348.

EMMEL, T. C. & J. F. EMMEL. 1962. Ecological studies of Rhopalocera in a Sierran community—Donner Pass, California. I. Butterfly associations and distributional factors. J. Lepid. Soc. 16: 23–44.

GARTH, J. S. 1928. Report of the Lorquin Entomological Society of Los Angeles. Proc. So. Calif. Acad. Sci. 27: 93–94.

GARTH, J. S. & J. W. TILDEN. 1963. Yosemite butterflies. J. Res. Lepid. 2: 1–96.

HALL, E. R. 1946. Mammals of Nevada. Univ. Calif. Press, Los Angeles.

HARPER, K. T., D. C. FREEMAN, W. K. OSTLER & L. G. KLIKOFF. 1978. The flora of Great Basin ranges: diversity, sources, and dispersal ecology. Great Basin Nat. Mem. 2: 81–103.

JOHNSON, N. K. 1965. The breeding avifaunas of the Sheep and Spring ranges in southern Nevada. Condor 67: 93–124.
——— 1975. Controls of number of bird species on moɪ ne islands in the Great Basin. Evolution 29: 545–567.
TIDWELL, K. B. & C. J. CALLAGHAN. 1972. A checklist of Uᶠ . butterflies and skippers. Mid-Continent Lepid. Series 4, no. 51: 1–16.
VAN ROSSEM, A. J. 1936. Birds of the Charleston Mountaiᵛ Nevada. Pac. Coast Avifauna 24: 1–65.

TWO SECONDARY PARASITOIDS OF THE PUSS MOTH, MEGALOPYGE OPERCULARIS

Earlier I reported (Khalaf 1975, Biology of the Puss Caterpillar and its Ichneumonid Parasite, Loyola Univ. Press, New Orleans, Louisiana, 43 p.) that the ichneumonid wasp, *Lymeon orbus* (Say), was a parasite of another ichneumonid, *Lanugo retentor* (Brullé), which, in turn, was a primary parasite of the megalopygid moth, *Megalopyge opercularis* (Smith). Recently, two other wasps were found to be secondary parasites of this moth.

On 30 March 1979, tiny eulophid wasps, *Dimmockia incongrua* (Ashm.), started to emerge in the laboratory from a cocoon of *Megalopyge*, which was obtained a few days earlier from New Orleans. The wasps emerged by eating one tiny hole about 1 mm in diameter in the shell of the cocoon. Thirty females and 2 males were recovered. Dissection of the cocoon revealed that the *Dimmockia* developed within the larval cell of *Lanugo retentor* (Brulle), a primary parasite of the moth. The *Lanugo* larva walled off the host *Megalopyge* prepupa, and then it was parasitized by *Dimmockia*, which caused the death of the *Lanugo* larva. Several brownish yellow pupal skins of the hyperparasite were left behind within the *Lanugo* cell.

A eupelmid wasp, *Arachnophaga aureicorpus* (Girault), emerged on 5 April 1979 from a *Megalopyge* cocoon that was collected in New Orleans in March 1979. The parasitized cocoon lacked the typical hard and tough texture of a finished cocoon; this lack is a symptom of tachinid fly parasitism, which inhibits the *Megalopyge* prepupa from reinforcing the cocoon, which causes the cocoon to harden. The emergence hole was 1.4 mm in diameter and was in a *Lanugo* cell containing a dead adult. Multiparasitism existed between *Lanugo* and tachinid flies before the eupelmid wasp attack. The *Lanugo* larva had walled off the *Megalopyge* prepupa and two tachinid puparia. No special cell was seen which might have belonged to the eupelmid wasp. This is a case of hyperparasitism following multiparasitism.

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GENERAL NOTES

AN OVIPOSITION "MISTAKE" BY *PAPILIO GLAUCUS* (PAPILIONIDAE)

Oviposition "mistakes," in which female butterflies lay eggs on plants toxic to their larvae, are well-documented and not infrequent occurrences (Hefley 1937, J. Anim. Ecol. 6: 138–144; Straatman 1962, J. Lepid. Soc. 16: 99–103; Sevastopulo 1964, ibid. 18: 104; Bowden 1971, ibid. 25: 6–12; Chew 1977, Evolution 31: 568–579; Young 1979, J. Lepid. Soc. 33: 56–57). Such mistakes usually occur after some sort of ecological disturbance, particularly when plants that share a chemical or taxonomic similarity with native hosts are introduced into an area where the butterflies are common. In the present instance, however, I discovered an oviposition mistake involving native insects and native plants.

On 13 June 1979, I found two eggs of *Papilio glaucus* L. (Papilionidae) on leaves of *Angelica atropurpurea* (Umbelliferae), growing in a swampy area adjacent to a plowed field. Though rosaceous shrubs were present within 10 ft of the angelica, the foliage was not intermingled. After the eggs hatched on 18 June, I placed one larva on leaves of *Prunus serotina* (Rosaceae), a well-known and ubiquitous host of *Papilio glaucus*, in order to confirm the identification of the caterpillars as *P. glaucus*. The caterpillar began to feed immediately on *Prunus serotina* and developed normally. The remaining larva was confined on leaves of *Angelica atropurpurea* and allowed to feed *ad libitum*; leaves were replaced daily. Although the larva fed daily, as evidenced by leaf damage and production of fecal pellets, it failed to develop beyond the second instar and eventually died on 9 July 1979. By contrast, the larva that had been placed on cherry after hatching had reached the fourth instar by that date.

The fact that the ovipositing female *Papilio glaucus* failed to reject *Angelica atropurpurea* as an unsuitable host is curious in that, in growth form and leaf shape, *A. atropurpurea*, a herbaceous perennial with 2- or 3- ternately compound leaves, bears little or no resemblance to any of the local *P. glaucus* hosts, including *Prunus, Acer, Betula, Crataegus, Fraxinus, Lindera, Liriodendron, Magnolia, Malus, Populus, Ptelea, Salix, Sassafras, Syringa* and *Tilia* (Scriber 1972, J. Lepid. Soc. 26: 235–236; Scriber, Lederhouse & Contardo 1975, ibid. 29: 10–14; Tietz 1972, An Index to the Described Life Histories, Early Stages and Hosts of the Macrolepidoptera of the Continental United States and Canada, A. C. Allen, Sarasota, Florida). *A. atropurpurea*, however, does share several chemical similarities with *P. glaucus* hosts. Like plants in the Magnoliaceae, Oleaceae, Rosaceae, Rutaceae and Tiliaceae, *A. atropurpurea* contains hydroxycoumarin compounds (Hegnauer, 1964–1973, Chemotaxonomie der Pflanzen, Vols. 3–6, Birkhauser Verlag, Basel, Switzerland). Although the remaining host families of *Papilio glaucus* are not reported to contain hydroxycoumarins *per se*, they almost all contain *p*-coumaric acid, the universal biosynthetic precursor of hydroxycoumarins. Because *Papilio polyxenes* Fab., a species not closely-related taxonomically to *P. glaucus* but sympatric with it over much of its range, feeds almost exclusively on the coumarin-rich Umbelliferae, including *Angelica atropurpurea* (Tietz 1972, *op. cit.*), it would be interesting to investigate the significance of coumarin compounds and biosynthetically related compounds as oviposition and feeding stimulants in the Papilionidae and to determine, if possible, whether the use of such chemical signals represents convergence or common ancestry within the genus *Papilio*.

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LONG DISTANCE DISPERSAL BY *CALLOSAMIA PROMETHEA* (SATURNIIDAE)

Shapiro (1977, J. Lepid. Soc. 31: 202–203) notes the importance of reporting well-documented, long range dispersal by Lepidoptera. Our experiments, involving release-recapture of painted male *Callosamia promethea* (Drury) (Sternburg et al. 1975, Science 195: 681–683; Jeffords et al. 1979, Evolution 33: 275–286; Toliver et al. in prep.) at two locations in central Illinois, have provided us with the opportunity to record two such instances. In both cases, the exact distance traveled and the time required to make the trip are known.

On 8 August 1977, MRJ released yellow and black painted male *C. promethea* at Robert Allerton Park, Piatt Co., Illinois. On 10 August 1977, MET collected a yellow painted male from this release in a trap baited with virgin females located at 614 W. Florida, Urbana, Champaign Co., Illinois. The second instance involved a wild male (unpainted) attracted to caged females at MET's apartment located in Tolono, Champaign Co., on 7 August 1978. This male was captured and marked on the underside of the left hindwing with the letter A, then released immediately. On 9 August 1978, it was recaptured at a trap located at 1101 S. Webber in Urbana.

In the first instance, the painted male traveled a distance of 36.5 km in 3 days (the equivalent of 3 afternoon flight periods; see Toliver et al. 1979, J. Lepid. Soc. 33: 232–238). Weather during the period 4–11 August 1977 was unsettled, with thunderstorms occurring daily (weather data from Urbana provided by the Illinois State Water Survey). Wind recorded as averaged 8.6 ± 1.6 km/hr from SW for the period 3–10 August. The release site in Allerton is located SW of the recapture site, upwind of the prevailing wind direction for the period during which the male was on the wing. Weather records show that on 11 August, wind direction shifted from SW to NE, indicating the passage of a front. Therefore, it appears probable that this male's dispersal flight was aided by storms moving through the area. Horsfall et al. (1973, Bionomics and Embryology of the Inland Floodwater Mosquito *Aedes vexans*, Univ. of Ill. Press, Urbana, 211 p.) notes, that *Aedes vexans* (Meigen) (Diptera, Culicidae) were transported long distances by cold fronts, and there are numerous examples of Lepidoptera being transported by storms (e.g., Neck 1978, J. Lepid. Soc. 32: 111–115).

The second male traveled 14 km in 3 days. The period 7–9 August 1978 was characterized by clear to partly cloudy skies in Urbana, no precipitation, winds from the W–SW at 8.2 ± 2.2 km/hr, and mean daily temperatures from 21.7 to 23.9°C. Wind direction shifted on 10 August from SW to E, again indicating the passage of a front, although in this case there was very little storm activity (trace of rain, partly cloudy skies on 10 August). Tolono is located S–SW of the Urbana recapture site; again, upwind of the prevailing wind direction.

The yellow-painted male released at Allerton Park had considerable wing damage, mostly in the form of a beak-shaped tear in the right forewing and another large block of missing wing area below the apex of the left forewing. The hindwings were relatively undamaged. This male would fall into wing-damage category VI (2.01 to 4.00 cm² of wing area missing) following the classification of Jeffords et al. (1979, Evolution 33: 275–286). The unpainted male released at Tolono was only slightly damaged (0.17 cm² of wing area missing, category II of Jeffords et al.). The nature of the wing damage of the painted male and the lack of significant wing damage in the unpainted male indicates that male *promethea* can travel considerable distances without wear on their wings. Thus, the capture of a reasonably undamaged male does not necessarily indicate that the male originated locally.

These events show that *C. promethea* is capable of long range dispersal, aided by prevailing winds and storms. The recording of two such events in two years indicates that such dispersal may not be a rare occurrence in *promethea*. This in turn implies that gene flow between populations in central Illinois may be considerable, despite the fact that such populations are otherwise isolated by surrounding agricultural lands.

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AN UNUSUAL OVIPOSITION SUBSTRATE FOR *HESPERIA OTTOE* (HESPERIIDAE) IN SOUTHWESTERN MINNESOTA

Published information on the life history of *Hesperia ottoe* Edwards gives fall witch-grass, *Leptoloma cognatum* (Schult.) Chase, as the oviposition substrate and larval host for populations in Michigan (Nielsen 1958, Lepid. News 12: 37–40; Nielsen 1960, J. Lepid. Soc. 14: 57). I report the use of a different and unusual oviposition substrate in southwestern Minnesota in 1978 and 1979.

Observations were made approximately 2.8 km SW of the town of Lake Benton, Lincoln Co., in a deeply dissected region of a prominent terminal moraine. Prior to its acquisition by The Nature Conservancy in 1978, the site was heavily grazed by domestic livestock. The vegetation on the steeply rolling upland *ottoe* habitat here is dry–mesic native grassland dominated by midgrass species.

Hesperia ottoe females oviposited on inflorescences of the pale purple coneflower, *Echinacea pallida* Nutt. (nomenclature according to Gleason & Cronquist 1963, Manual of Vascular Plants of Northeastern United States and Adjacent Canada), which were also used by males as perching sites from which mate-locating flights were launched, and by both sexes as their major nectar source. Ova were usually placed among the stiff spiny receptacular bracts which extend beyond the disk flowers they subtend (Fig. 1), though a few eggs were observed near the base of ray flowers. The majority of inflorescences had a single egg, but two were frequently present, and as many as five were occasionally seen.

The purple coneflower is almost certainly not a larval host; all hosts observed at this site were grasses (Poaceae), as are all known hosts for the genus (MacNeill 1975, in Howe (ed.), The Butterflies of North America, p. 464). No larval feeding on the cone-flower was observed; larvae dropped off the inflorescences into the grasses (usually a few cm below) as soon as they hatched and finished eating the chorion. Females were occasionally observed ovipositing on host grasses (four species), and one oviposition

FIG. 1. Closeup of disk of *Echinacea pallida* inflorescence with two ova of *Hesperia ottoe* (center of photograph), showing typical placement. Ray flowers are visible in the lower part of the photograph. Scale line = 2 mm.

on the leaf of another forb was seen. Though no determination of the relative frequencies of utilization of various substrates was possible, oviposition on the coneflowers appears to be a major behavioral characteristic and not the result of "mistakes" or random choice. About 600 inflorescences with eggs were tagged during desultory inspection in 16 ha of habitat in 1978, and a sampling program in 32 ha in 1979 revealed several times that number with ova on them. Ova were found on coneflowers at two other sites in southwestern Minnesota in 1978 and in several pastures near the study site in 1979. No evidence of oviposition by females on other flowers was found.

This use of a non-host oviposition substrate is reminiscent of the behavior of some populations of *Hesperia lindseyi* Holland reported by MacNeill (1964, Univ. Calif. Publ. Entomol. 35: 1–130) which oviposit on an arboreal lichen. The selective pressures responsible for the behavior in *H. ottoe* are unknown. Domestic livestock avoid grazing the evidently unpalatable coneflower as presumably bison did, and it may be that larvae in the immediate vicinity of these plants are thus less likely to be trampled or eaten by large ungulates. *H. ottoe* is known to occur in the absence of *Echinacea pallida* (e.g., a colony in southeastern Minnesota in a relict sand dune habitat, and Michigan populations), and it may be that the distribution of the behavior will provide a clue to its significance. It is hoped that this note will alert observers elsewhere to look for the behavior.

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POLYMORPHISM IN LARVAE OF *CATOCALA BLANDULA* (NOCTUIDAE)

On 25 April 1979 six larvae of *Catocala blandula* Hulst hatched from eggs laid by one female from Lebanon, New Jersey. They were fed on *Crataegus*. When in the

ultimate larval stage, 13 May, I found three larvae of the regular grayish-brown form, and three larvae of the same color and markings, but with a broad brown, dorsal, longitudinal band reaching from the prothorax to the last abdominal segment. Only in the last larval instar was this difference in the larvae detected. The 1:1 ratio of the two larval morphs suggests that the presence or absence of dorsal banding is under simple genetic control, i.e., a single autosomal locus having two alleles may control the presence or absence of the brown banding. One larva of each form has been inflated (Figs. 1 & 2). The two larvae of each form pupated and emerged as adults. From 13 to 18 June both sexes of adults emerged from both larval forms. When these moths were compared with each other, no phenotypic differences were detected. More rearings of this species will be done in the future.

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FIGS. 1 & 2. 1, usual grayish larva of *C. blandula*; 2, brown striped larva of *C. blandula*. Both are last instar larvae.

THE FIRST CAPTURE OF *APPIAS DRUSILLA* (PIERIDAE) IN COLORADO

On 5 August 1979, D. L. Barlow took a battered female specimen of *Appias drusilla neumoegenii* Skinner in a mountain valley near the town of Santa Maria, Park Co., Colorado, at elev. 8400 ft (2560 m). This tropical butterfly breeds in the extreme southern parts of the United States, and adults are prone to long range wanderings; they regularly occur in areas far north of their normal breeding grounds. Strays have been reported from as far north as Nebraska, and there is a sight record by F. M. Brown from El Paso Co., Colorado, on 7 July 1941 (1942, Entomol. News, 53: 82–83). This is, however, the first reported capture (Fig. 1) of this species in the state, and only the second record from the entire Rocky Mountain region north of the 35th parallel.

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FIG. 1.   Specimen of *Appias drusilla* captured in Park Co., Colorado, on 5 August 1979.

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JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

14 December 1981

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Cover Illustration: Adult male *Anthocharis sara* Lucas (Pieridae) on inflorescence of fiddleneck (*Amsinckia intermedia* Fischer & Meyer, Boraginaceae). These butterflies occur in central Arizona during spring, often flying through small canyons and washes. Their larvae feed on a wide variety of mustards (Cruciferae). Original drawing by Dr. Rosser W. Garrison, Calle Iris UU18B, Rio Piedras, Puerto Rico 00926.

Journal of

The Lepidopterists' Society

PRESIDENTIAL ADDRESS 1980

ON THE ACHROMATIC *CATOCALA*[1]

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Most of the nearly 100 species of *Catocala* Schrank (underwing moths, Noctuidae) that occur in North America are characterized by colorful, banded hindwings, which contrast strikingly with bark-like cryptic forewings. Some 20 species, however, have no trace of color or banding on the uppersides of the hindwings, these structures being entirely black (except for a contrasting white fringe in some species). The species having black hindwings (Table 1) are referred to as the achromatic (as opposed to chromatic) *Catocala*, and they have long held a special appeal to collectors. This appeal is reflected in the romantic, though doleful, names that many species bear—e.g., the widow underwing (*C. vidua* Smith & Abbot), the dejected underwing (*C. dejecta* Strecker), the inconsolable underwing (*C. insolabilis* Gn.) (Fig. 1).

There is general agreement that the achromatic *Catocala* are a series of distinct species that have evolved secondarily from species with chromatic hindwings (Grote, 1872; Hulst, 1880; Holland, 1903; Barnes & McDunnough, 1918; Forbes, 1954), but there has been considerable question as to the functional significance and mode of origin of the black hindwing pattern (Sargent, 1969, 1976, 1978; Kettlewell, 1973). I propose to explore these issues here, considering first the matter of function and then the origin of achromatic species from chromatic ancestors.

Kettlewell (1973, p. 215) contended that the *Catocala* with black

TABLE 1. The achromatic *Catocala* of North America.

Group[1]	Foodplants	Species
III	Juglandaceae	*epione*
V	Juglandaceae	*robinsoni, judith, flebilis, angusi, obscura, residua, sappho, agrippina*
VI	Juglandaceae	*retecta, dejecta, ulalume, insolabilis, vidua, maestosa, lacrymosa*
XV	Ericaceae	*andromedae*
XVII	Rosaceae	*miranda, orba*

[1] Subdivisions of the genus, after Forbes (1954).

hindwings have "forfeited their flash coloration. . . ." and so have ". . . abandoned a major mechanism of defence." However, there is considerable evidence that achromatic hindwings, like chromatic hindwings, will elicit startle reactions in birds. The primary evidence for this startle effect is provided by *Catocala* specimens bearing crisp beak imprints on their wings (Type III damage—Sargent, 1973, 1976). Such specimens are regularly taken in large samples of these moths,
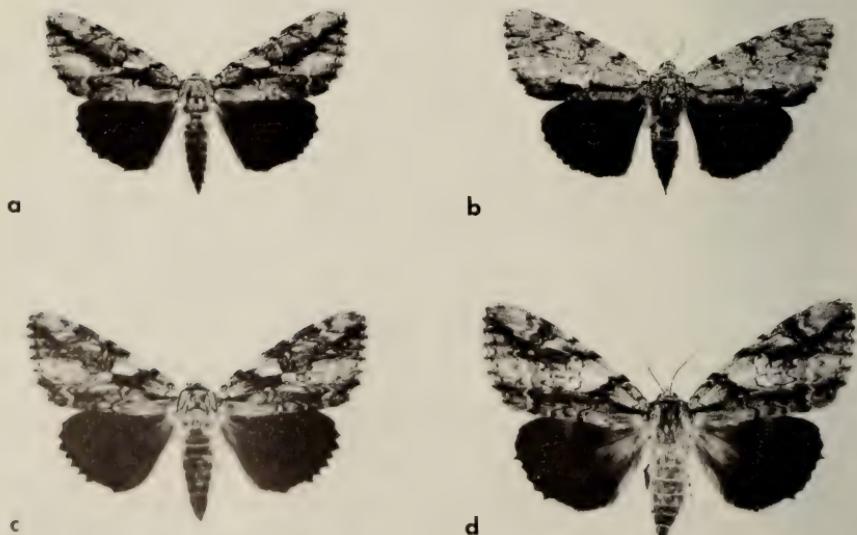
FIG. 1. Representative achromatic *Catocala* species. **a.** *flebilis*; **b.** *insolabilis*; **c.** *dejecta*; **d.** *vidua*. (ca. 0.55×)

and beak imprints are at least as frequently found on achromatic as on chromatic individuals (Sargent, 1973).

The Type III damage pattern apparently results when a bird is momentarily startled by the appearance of a brightly colored or boldly patterned hindwing and relaxes its grip on a captured moth (Sargent, 1973). I have proposed previously that hindwing diversity, and particularly the contrast between chromatic and achromatic patterns, introduces the element of anomaly (the unexpected) into the predator-prey system involving birds and these moths. Anomaly then acts to interfere with the avian counteradaptation to startle effects—habituation. Habituation is defined as "the waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement" (Thorpe, 1963). Habituation requires a series of encounters with a specific stimulus, and encounters with sufficiently different stimuli are known to interfere with, or abolish, the development of an habituated response (Donahoe & Wessells, 1979). This "dishabituation" phenomenon provides, I believe, a selective basis for the evolution of hindwing diversity, particularly the distinctively different achromatic patterns, in the *Catocala* (Sargent, 1973, 1976, 1978, 1980).

As a specific example let us take *C. neogama* Smith & Abbot (orange and black banded hindwings) and *C. retecta* Grt. (black hindwings) (Fig. 2), two Juglandaceae-feeding species that are often encountered in the same habitats. It is assumed that habituation to the hindwings will proceed so long as only one of these two species is being encountered (say, *C. neogama*). At some point, perhaps after from 3 to 6 encounters, based on prior studies (Blest, 1957; Coppinger, 1969, 1970), the startle response will disappear and a bird would be able to capture individuals of that species. Now, however, if the other species (here, *C. retecta*), with its closely similar forewings, were encountered, the new hindwing would elicit startle again. Habituation to this new stimulus would again require a series of encounters, and this might or might not occur, depending on the frequencies of *C. neogama* and *C. retecta* in the environment. This situation has been analyzed in more detail elsewhere (Sargent, 1981), but it is apparent that the two species would substantially benefit one another with respect to startle as long as they were about equally common, and that the rarer of the two species would always derive a greater benefit from their co-occurrence. Birds would then exert frequency dependent selection on the moths, tending, thereby, to promote long-term stability of the two species at near equal numbers.

This reasoning has been based on the assumption that a bird cannot distinguish *C. neogama* and *C. retecta* in the resting (cryptic) state.

If that distinction were possible, then a bird might come to associate one forewing pattern with orange and black banded hindwings; another forewing pattern with entirely black hindwings; and habituate to both hindwings on the basis of these predictable associations. This possibility may explain why so many achromatic species in North America have forewings that are remarkably similar to those of certain chromatic species with which they co-occur. I have proposed previously (Sargent, 1969) that predator selection would favor the development of forewing similarities in species having very different hindwings, since, if the forewings were indistinguishable, they would provide no clue to the underlying hindwing patterns.

Examination of the *Catocala* fauna of North America reveals some striking forewing similarities between certain species having achromatic hindwings and others having chromatic hindwings. In some cases the species involved are known to be closely related (e.g., *C. judith* Strecker and *C. serena* W. H. Edw., *C. epione* (Drury) and *C. consors* (Smith & Abbot)) (Fig. 2). In these cases the foodplants are the same, as are the patterns of seasonal occurrence, and often the behaviors associated with crypsis (selection of resting sites, orientation, etc.) (Sargent, 1969, 1976, 1978). One of the most remarkable pairings of this sort is that of *C. lacrymosa* Gn. and *C. palaeogama* Gn., where the two species occur in a striking, parallel series of forewing morphs (Remington, 1958) (Fig. 3). On the other hand, there are some cases of close forewing resemblance involving achromatic and chromatic species that are not closely related (e.g., *C. robinsoni* Grt. and *C. concumbens* Wkr., *C. maestosa* (Hlst.) and *C. marmorata* W. H. Edw.) (Fig. 4). The two species in these cases feed on very different foodplants, but there is some evidence to suggest that their patterns of seasonal occurrence and resting habits may be very similar (Sargent, 1976; J. Bauer, pers. comm.).

These examples of forewing similarities in species with chromatic and achromatic hindwings, particularly when considered in light of the evidence that such species commonly co-occur in the same environments, strengthen the argument that achromatic hindwings function as startle devices on the basis of their contrast with chromatic hindwing patterns. Now, however, we are faced with a most perplexing question. If some species benefit by co-existing with other species having different hindwing patterns, why has no species adopted what would seem a simpler means of ensuring that co-existence, i.e., by becoming polymorphic with respect to the hindwings?

A few trivial hindwing variants have received names, e.g., form "normani" of *C. ilia* (Cramer), which shows some extension of black scaling along the veins, or form "sinuosa" of *C. coccinata* Grt., show-
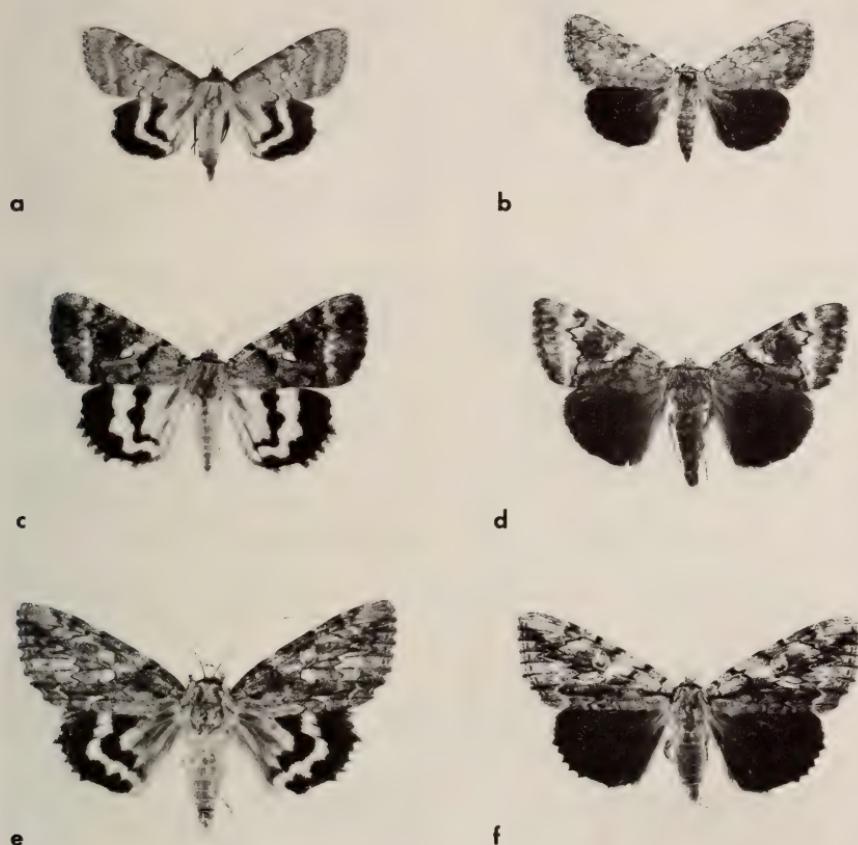
FIG. 2.   Pairs of Juglandaceae-feeding *Catocala* species having similar forewings, but chromatic and achromatic hindwings. **a, b.** *serena* and *judith*; **c, d.** *consors* and *epione*; **e, f.** *neogama* and *retecta*. (ca. 0.55×)

ing a reduction in the width of the inner band, characteristic of southern specimens. And occasional mutants with very aberrant hindwings do occur. Even an entirely black hindwing may turn up in a species whose hindwings are normally chromatic (e.g., ab. "fletcheri" of *C. unijuga* Wlk., or the recently described ab. "sargenti" of *C. micronympha* Gn. (Covell, 1978) (Fig. 6). These exceptions are exceedingly rare, however, and constancy is certainly the rule with respect to the hindwings within any species. What selective factor(s) would promote such constancy?

One might suggest that the hindwings are mimetic in some way
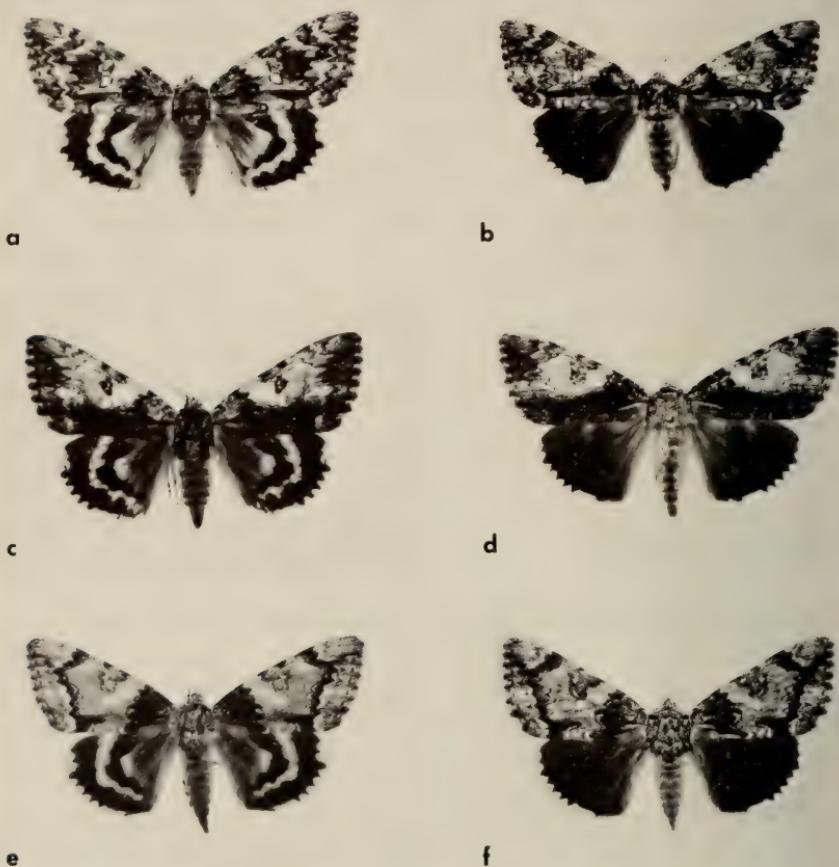
FIG. 3. Parallel forewing morphs in *C. palaeogama* (left) and *C. lacrymosa* (right). **a, b.** typical, typical; **c, d.** "annida," "evelina"; **e, f.** "phalanga," "zelica." (ca. 0.55×)

and have been selected for closeness of resemblance to various models. However, *Catocala* hindwings bear no clear resemblance to known noxious or unpalatable prey items or to dangerous or threatening predators; rather, the hindwings seem to function simply as startle devices in anti-predator contexts. It is possible that this startle function will account for some of the uniformity we see. Certain combinations of colors, contrasts, and edges may, because of operational properties of the visual and nervous systems of predators, produce a maximal startle effect. It may be that the banded and entirely black *Catocala* hindwing patterns are particularly effective startle stimuli. This, however, will not explain the lack of intraspecific variation in
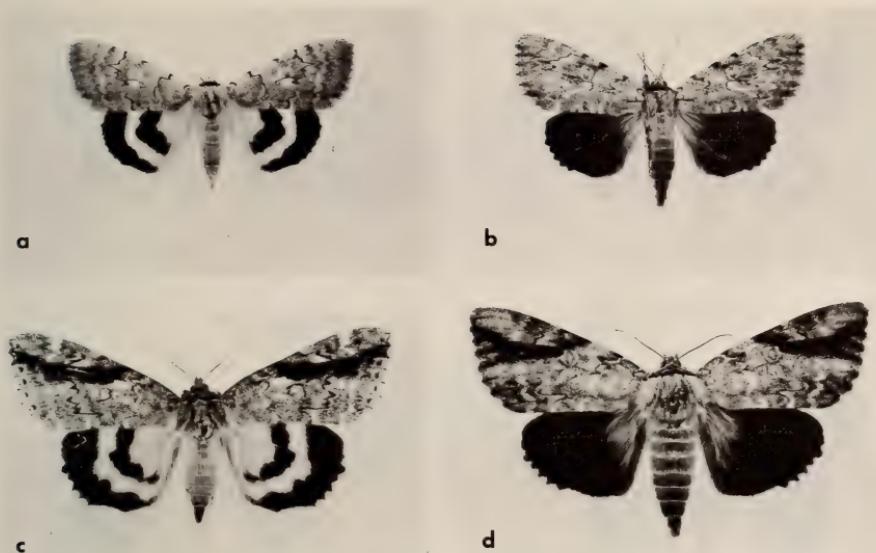
FIG. 4. Pairs of *Catocala* species having similar forewings, but chromatic and achromatic hindwings, and feeding on different foodplants. **a, b.** *concumbens* (Salicaceae) and *robinsoni* (Juglandaceae); **c, d.** *marmorata* (Salicaceae) and *maestosa* (Juglandaceae). (ca. 0.55×)

the hindwings, as there are many variations across species, each of which is presumably an effective startle stimulus.

Actually, this problem of interspecific hindwing diversity plagues any effort to explain hindwing uniformity within species in terms of effects on predators. We are forced, I believe, to consider a selective factor that would operate *within* each species to promote an invariant

TABLE 2. The numbers and frequencies of chromatic and achromatic Juglandaceae-feeding *Catocala* in Robinson Trap samples taken over one or more entire seasons at several locations (1961–1979).

Locations (no. years)	Chromatic		Achromatic	
	Species	No. (%)	Species	No. (%)
Washington, CT[1] (12)	6	3603 (60)	8	2406 (40)
Leverett, MA (10)	4	473 (39)	7	728 (61)
W. Hatfield, MA[2] (10)	5	960 (49)	8	998 (51)
Sturbridge, MA[3] (2)	4	73 (46)	6	85 (54)
Geo. Reserve, MI[4] (1)	4	138 (34)	6	268 (66)
Amherst, MA[5] (1)	6	93 (46)	7	110 (54)
Totals	6	5340 (54)	9	4595 (46)

Data courtesy of S. A. Hessel[1], C. G. Kellogg[2], C. C. Horton[3], D. Owen[4], and F. A. Vaughan & L. P. Brower[5] (two traps).
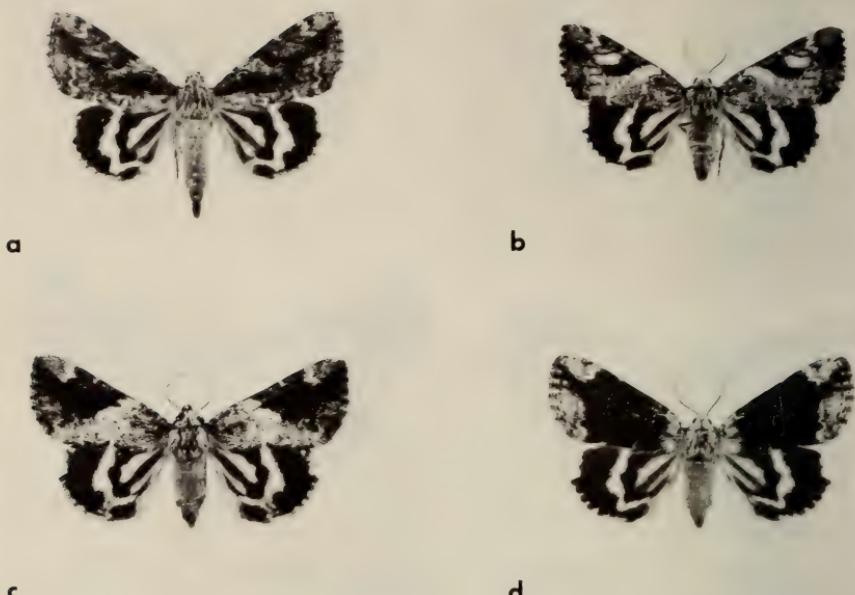
Fig. 5. Forewing morphs of *C. micronympha*. **a.** typical; **b.** un-named; **c.** "hero"; **d.** "grisela." (ca. 0.80×)

hindwing pattern. Such selection would occur if the hindwings function as specific recognition devices, playing a role in courtship and mating, and so serving as isolating mechanisms within the genus.

The contention that *Catocala* hindwings may play a role in the sexual interactions of the moths themselves seems unreasonable in some ways. *Catocala* are nocturnal, as far as is known, and visual communication, particularly if colors are involved, seems prohibited at night. Furthermore, *Catocala* males presumably locate females by chemical signals (pheromones), and it seems likely that the males also elaborate pheromones (Bailey, 1882) which could be the basis for acceptance or rejection of the males by the females.

On the other hand, very little is actually known regarding courtship and mating in these moths. Only *C. relicta* Wlk. has been mated in captivity (Sargent, 1972), and while these moths were reported to mate at night, it was also noted that courtship involved considerable male activity ("walking and flying about the cage") and that the hindwings of both partners were exposed when the moths came into sexual contact. Perhaps some courtship activities of the *Catocala* are restricted to bright, moonlit conditions? It is also possible that court-

FIG. 6.   *C. micronympha* "gisela" (**above**) and an aberration, "sargenti," with achromatic hindwings (**below**). (ca. 0.80×)

ship activities in some species are initiated during crepuscular periods or even during daylight. David Baggett has reported instances of males of *C. insolabilis* Gn. aggregating about a female during the late afternoon in Florida (pers. comm.).

Certainly we need more information on the reproductive behaviors of the *Catocala*. For the moment, however, I think we cannot rule out the possibility that the *Catocala* use their hindwings as species-specific visual signals during courtship. Such a possibility would provide the intense stabilizing selection that seems required by the hindwing uniformity that exists within each *Catocala* species.

Let us now return to the achromatic hindwings and consider specifically the question of their origin. My discussion to this point indicates that the black hindwing pattern is an effective startle device, at least when present along with chromatic hindwings, but that it might be selected against in mating. Yet, there are some 20 *Catocala* species with black hindwings, most of which appear to have evolved independently from chromatic ancestors. How have these speciation events occurred?

We have seen that the achromatic hindwing pattern can arise in a single step, since occasional specimens of normally chromatic species have all traces of hindwing color obliterated by black scaling. Such

specimens are exceedingly rare, but they must represent a first step in the sort of speciation process that we are considering. Usually, no doubt, such specimens die without leaving progeny, but they must occasionally persist. And when they do persist, they must rapidly achieve species status, as the black hindwing pattern does not occur as a morph in any extant species.

The classical allopatric model of speciation seems entirely inade-quate to account for this situation. Certainly, it seems most unlikely that achromatic hindwings arose in isolated subpopulations and that these subpopulations remained isolated long enough to acquire ge-netic differentiation sufficient to enable their members to re-invade the ranges of the parent populations as full species. Why would isolated populations acquire achromatic hindwings in the first place, especially in view of the evidence which suggests that achromatic hindwings are most effective as startle devices when they co-occur with chromatic hindwings? And if one postulates the founding of these isolated populations by individual females, who happened to be mutants with black hindwings, is it conceivable that this event could have occurred on several separate occasions, given the great rarity of such mutants in chromatic species? And even if that were granted, is it likely that each of the achromatic subpopulations would by chance remain isolated until species status was achieved?

Another allopatric scenario might be based on the assumption that achromatic hindwings arose as anti-hybridization devices after specia-tion, and re-invasion events had led to the co-occurrence of similar chromatic species. But is it likely that this particular anti-hybridization device would arise by chance on so many occasions? And how would one account for the spread of the achromatic trait into areas of non-overlap of the hybridizing species?

It seems more likely to me that individuals with achromatic hind-wings have become new species while co-occurring with their paren-tal species with chromatic hindwings. This, however, is sympatric speciation—a controversial concept indeed (see Mayr, 1963; Maynard Smith, 1966; Bush, 1975). In this case, we must posit some mechanism which restricts the matings of individuals with achromatic hindwings to other achromatic individuals (homogamy).

We might invoke a second, coincidental mutation that would affect some aspect of the mate selection process such that individuals with achromatic hindwings could only mate with one another. However, this would require the simultaneous occurrence of two individuals of opposite sex, both of whom had the mutation for achromatic hind-wings *and* the mutation for altered mating preferences, and this un-

likely event would have had to occur many times over in order to account for the present achromatic species.

A pleiotropic effect of the mutation for black hindwings on some aspect of mate selection would strain credulity a little less, for in this case every individual with black hindwings might only be able to mate with another black-hindwinged individual. This pleiotropic effect could conceivably involve a change in hindwing preference, though a change in something like the timing of emergence or mating readiness would seem more likely. In this way, a mating between siblings with black hindwings might occur, even with the seeming impediment of inappropriate hindwings, given that no other mates might be available at a changed mating time. An initial sib mating of this sort might provide sufficient progeny to initiate selection for an altered hindwing preference in mating.

This scenario is essentially a case of instantaneous speciation, a concept that has been extensively criticized by many evolutionary biologists (see Mayr, 1973, p. 432 ff.). Mayr has pointed out (1973, p. 472) that, ". . . a species would lose all the advantages of improved utilization of the environment through adaptive polymorphism if it were to split into a series of narrowly specialized species." Yet, in a sense, the *Catocala* have done just that. Many species occur as "narrowly specialized species" (differing in hindwing patterns) in the same environments. Hindwing polymorphisms would seem to be a more efficient and adaptive means of creating the diversity we see, but hindwing polymorphisms do not occur.

Thus, unlikely as the sympatric speciation model may be, I believe that it provides a more plausible explanation of the existing *Catocala* situation with respect to achromatic hindwings than does an allopatric model. Plausibility, however, like beauty, may lie in the eye of the beholder. Is there any evidence we might obtain that would enable a better judgment of the arguments I have advanced?

I would like to conclude by suggesting two lines of investigation that might provide such evidence. The first of these involves mating these moths. We must find the secret to obtaining this behavior in captivity. Once done, we should be able to determine whether the hindwings do play a role in mate selection, and if so, what kinds of alterations interfere with that process. We should also be able to determine whether the species with achromatic hindwings have different pheromones or courtship behaviors than their closely related chromatic species, or whether they differ only with respect to the time of day at which they mate. If such studies indicated that the achromatic species are isolated from their chromatic relatives by a consistent,

single characteristic, this might support the argument for their origin by a series of similar sympatric speciation events, rather than by a number of separate allopatric events.

The second line of investigation I would recommend involves the technique of protein electrophoresis (for a lucid discussion of this method and the rationale underlying its use and application, see Futuyma, 1979). Use of this technique might reveal extremely close relationships between certain achromatic and chromatic species; closer, perhaps, than any other relationships within the genus. Such a finding would again support the sympatric hypothesis, regarding the origin of the achromatic species. Also, since the sympatric speciation process could occur anywhere within the range of a parent population, then speciation might occur more frequently than allopatric models would predict. This could be reflected in electrophoretic data suggesting close groupings of species having one chromatic member and two or more achromatic members.

These sorts of investigations may permit some assessment of the rather unconventional ideas that I have advanced. I would stress, however, that many other kinds of studies should be carried out as well. The life histories of a number of species have not been recorded (see Sargent, 1976). We know almost nothing of the competitive interactions among larvae of species feeding on the same foodplants. Recorded observations of predation on the moths, either under field or captive conditions, are virtually non-existent. In short, we need more information on all aspects of the biology of the *Catocala*. And as our knowledge of these insects increases, so too must our understanding of their patently complex evolutionary history. I suspect that many exciting discoveries await our closer attention.

I wish to thank Victoría Borden Muñoz for the photographs of the moths.

LITERATURE CITED

BAILEY, J. S. 1882. Femoral tufts or pencils in certain Catocalae. Papilio 2: 51–52.

BARNES, W. & J. McDUNNOUGH. 1918. Illustrations of the North American species of the genus *Catocala*. Mem. Amer. Mus. Nat. Hist. 3(1). 47 pp. 22 pl.

BLEST, A. D. 1957. The evolution of eyespot patterns in the Lepidoptera. Behaviour 11: 209–256.

BUSH, G. L. 1975. Modes of animal speciation. Ann. Rev. Ecol. Syst. 6: 339–364.

COPPINGER, R. P. 1969. The effect of experience and novelty on avian feeding behavior with reference to the evolution of warning coloration in butterflies. Part I. Reactions of wild-caught adult blue jays to novel insects. Behaviour 35: 45–60.

——— 1970. The effect of experience and novelty on avian feeding behavior with reference to the evolution of warning coloration in butterflies. II. Reactions of naive birds to novel insects. Amer. Nat. 104: 323–335.

COVELL, C. V., JR. 1978. A new hindwing aberration of *Catocala micronympha* Guenée from Kentucky. J. Lepid. Soc. 32: 221–223.

CROZE, H. J. 1970. Searching image in carrion crows. Zeit. Tierpsychol. 5: 1–85.

DONAHOE, J. W. & M. G. WESSELLS. 1979. Learning, Language and Memory. Harper & Row, New York. 513 pp.

FORBES, W. T. M. 1954. Lepidoptera of New York and Neighboring States. III. Noctuidae. Cornell Univ. Agric. Exp. Sta. Mem. 329. 433 pp.

FUTUYMA, D. J. 1979. Evolutionary Biology. Sinauer, Sunderland, Mass. 565 pp.

GROTE, A. R. 1872. On the North American species of *Catocala*. Trans. Amer. Entomol. Soc. 4: 1–20.

HOLLAND, W. J. 1903. The Moth Book. Doubleday, New York. 424 pp.

HULST, G. D. 1880. Remarks upon the genus *Catocala*, with a catalogue of species and accompanying notes. Bull. Brooklyn Entomol. Soc. 3: 2–13.

KETTLEWELL, H. B. D. 1973. The Evolution of Melanism. Clarendon, Oxford. 424 pp.

MAYNARD SMITH, J. 1966. Sympatric speciation. Amer. Nat. 100: 637–650.

MAYR, E. 1963. Animal Species and Evolution. Harvard Univ. Press, Cambridge, 797 pp.

REMINGTON, C. L. 1958. Genetics of populations of Lepidoptera. Proc. 10th Int. Congr. Entomol. (1956) 2: 787–805.

SARGENT, T. D. 1969. A suggestion regarding hindwing diversity among moths of the genus *Catocala* (Noctuidae). J. Lepid. Soc. 23: 261–264.

―――― 1972. Studies on the *Catocala* (Noctuidae) of southern New England. III. Mating results with *C. relicta* Walker. J. Lepid. Soc. 26: 94–104.

―――― 1973. Studies on the *Catocala* (Noctuidae) of southern New England. IV. A preliminary analysis of beak-damaged specimens, with discussion of anomaly as a potential anti-predator function of hindwing diversity. J. Lepid. Soc. 27: 175–192.

―――― 1976. Legion of Night: The Underwing Moths. Univ. Massachusetts Press, Amherst. 222 pp.

―――― 1977. Studies on the *Catocala* (Noctuidae) of southern New England. V. The records of Sidney A. Hessel from Washington, Connecticut, 1961–1973. J. Lepid. Soc. 31: 1–15.

―――― 1978. On the maintenance of stability in hindwing diversity among moths of the genus *Catocala* (Lepidoptera: Noctuidae). Evolution 32: 424–434.

―――― 1980. Antipredator adaptations of underwing moths. Chapter 12 *in* A. Kamil and T. D. Sargent, eds., Foraging Behavior: Ethological, Ecological and Psychological Perspectives. Garland Press, New York. pp. 259–284.

―――― 1981. Studies on the *Catocala* (Noctuidae) of southern New England. VI. The "pairing" of *C. neogama* and *C. retecta*. J. Lepid. Soc. 35, in press.

SARGENT, T. D. & S. A. HESSEL. 1970. Studies on the *Catocala* (Noctuidae) of southern New England. I. Abundance and seasonal occurrence of the species, 1961–1969. J. Lepid. Soc. 24: 105–117.

THORPE, W. H. 1963. Learning and Instinct in Animals. 2nd ed. Harvard Univ. Press, Cambridge. 558 pp.

TINBERGEN, L. 1960. The natural control of insects in pine woods. I. Factors influencing the intensity of predation by song birds. Arch. Neerl. Zool. 13: 265–343.

THE GENUS *CATOCALA* SCHRANK COLLECTED FROM FOUR EASTERN SOUTH DAKOTA COUNTIES (NOCTUIDAE: CATOCALINAE)

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ABSTRACT. Twenty-eight species of underwing moths were collected from eastern South Dakota by the use of light traps and a technique for collecting *Catocala* moths known as sugaring. Included are data on flight period, time of collection and a key to the species.

The members of the genus *Catocala* Schrank are commonly called underwing moths. The genus is mostly temperate in distribution and according to Forbes (1954) contains about 200 species. Sargent (1976) listed 71 species east of the Mississippi River and McDunnough (1938) listed 104 North American species.

This paper treats 28 species of underwing moths, collected from four eastern South Dakota counties: Clay, Minnehaha, Lake and Brookings. Included are data on flight period, collecting methods, time of collection, and a key to species.

METHODS AND MATERIALS

Collecting included the use of light traps (black-light and standard 200 watt light bulb) and the use of a technique for collecting moths known as "sugaring" (a mixture of brown sugar and beer applied to trees). Two types of specimens have been used in this study: museum specimens deposited in the South Dakota State University collection, which contains the Truman collection from Volga, and specimens collected by the use of light traps and bait (sugaring) for the years 1976 through 1979 in Minnehaha Co. and 1979 in Brookings Co. Collecting in Minnehaha was by the use of white light and bait within the city of Sioux Falls, South Dakota. In Brookings Co. specimens were collected from five different light trap sites using a fluorescent black light, 15 watt General Electric bulb, $F_{15}T8$-BL. Three traps were placed in the city of Brookings; one trap a mile south of Volga; one trap east of Aurora.

Key to Eastern South Dakota *Catocala* Moths

1. Foretibiae spined _____ 2
   Foretibiae not spined _____ 7
2. Ventral forewing with postmedial band orange _____ 4
   Ventral forewing with postmedial band not orange _____ 3
3. Hindwing black _____ *insolabilis*
   Hindwing orange _____ *innubens*

Specimen Records:

    Catocala innubens Guenee (9 specimens): Brookings—VIII-28-76, ♂; Sioux Falls—VII-12-78, ♀; VIII-3-78, ♀; VIII-5-78, ♀; VIII-5-78, ♀; VII-29-79, ♂; VII-9-79, ♂; VIII-12-79, ♂; Volga—VII-7-1896, 2 ♀♀.

Catocala piatrix Grote (2 specimens): Brookings—VII-23-57, ♂; Vermillion—VII-16-46, ♂.

Catocala habilis Grote (2 specimens): Volga—VII-12-1896, ♂; VII-14-1896, ♂.

Catocala insolabilis Guenee (3 specimens): Sioux Falls—VII-24-79, 2 ♀♀; VII-26-79, ♂.

Catocala palaeogama Guenee (2 specimens): Sioux Falls—VII-15-79, ♀; VII-20-79, ♂.

Catocala neogama (Abbot and Smith) (9 specimens): Sioux Falls—VIII-13-77, ♀; VII-23-78, ♀; VII-3-78, 2 ♂♂, ♀; VIII-5-78, 2 ♂♂; VII-22-79, ♀; VIII-31-79, ♂.

Catocala ilia (Cramer) (5 specimens): Brookings—VII-29-69, ♀; Sioux Falls—VII-8-78, 2 ♀♀; VII-9-78, ♂; VII-12-78, ♀; Volga—reported as common (Truman, 1896), no specimens.

Catocala cerogama Guenee (3 specimens): Sioux Falls—VII-26-77, ♀; VII-25-78, ♂; VIII-5-78, ♀; Volga—reported rare (Truman, 1897), no specimens.

Catocala relicta Walker (no specimens): Volga—reported as very rare (Truman, 1897).

Catocala parta Guenee (71 specimens): Brookings—VII-20-70, ♀; VIII-9-70, ♂; Sioux Falls—VI-23-77, ♀; VI-23-78, ♀; VII-6-78, ♂; VII-8-78, ♂, 2 ♀♀; VII-9-78, 2 ♀♀; VII-12-78, ♂; VIII-3-78, ♀; VII-14-79, ♀; VII-15-79, ♂; VII-16-79, ♂; VII-18-79, 3 ♂♂, ♀; VII-19-79, 6 ♂♂, 4 ♀♀; VII-20-79, 7 ♂♂, 3 ♀♀; VII-22-79, 4 ♂♂, 4 ♀♀ FE; VII-24-79, 6 ♂♂, ♀; VII-27-79, ♂, ♀; VII-28-79, 2 ♂♂, 2 ♀♀; VII-29-79, ♀; VII-30-79, ♂; VIII-2-79, ♂; VIII-9-79, ♀; VIII-21-79, ♀; Volga—3 ♂♂, 3 ♀♀, no dates.

Catocala meskei Grote (13 specimens): Brookings—VIII-3-22, ♂; VII-9-66, ♀; VIII-1-66, ♀; VII-23-70, ♂; Sioux Falls—VII-9-76, ♀; VII-4-77, ♂; VII-29-78, ♀; VIII-6-79, ♂, ♀; VIII-15-79, ♂; VIII-19-79, ♂, ♀; VIII-21-79, ♂.

Catocala arizonae Grote (*stretchii* of authors) (no specimens): Volga—listed as rare (Truman, 1897).

Catocala luciana Hy. Edwards (26 specimens): Brookings—VIII-12-?, ♀; VII-24-14, ♂; VII-26-19, ♂; VIII-15-27, ♂; VIII-10-43, ♂; IX-13-57, ♂; VIII-19-70, ♂; IX-3-79, ♀; Chester—VII-12-23, ♂; VI-28-29, ♂; VII-27-29, ♂; VII-29-29, ♂; VIII-2-29, ♂; Sioux Falls—VII-20-77, ♂; VII-25-78, ♂; VIII-3-78, ♂, 2 ♀♀; VIII-16-78, ♂; VIII-12-79, ♂; VIII-20-79, ♂; IX-1-79, ♂; Volga—4 ♂♂, no dates.

Catocala concumbens Walker (2 specimens): Brookings—VII-6-66, ♂; Volga—♂, no date.

Catocala amatrix (Hübner) (5 specimens): Brookings—IX-6-79, ♀; Sioux Falls—VIII-20-78, ♀; VIII-6-79, ♂; VIII-18-79, ♂; VIII-21-79, ♀; 1 sight record VIII-28-78.

Catocala cara Guenee (4 specimens): Sioux Falls—VIII-3-78, ♂; VIII-17-79, ♂; 1 sight record IX-26-79; Volga—2 ♀♀, no dates.

Catocala abbreviatella Grote (2 specimens): Brookings—VI-25-77, ♂, ♀; Volga—recorded as rare (Truman, 1897), no specimens.

Catocala nuptialis Walker (4 specimens): Sioux Falls—VIII-3-78, ♂; VIII-16-79, ♂; VIII-29-79, ♀; IX-26-79, ♀.

Catocala whitneyi French (21 specimens): Brookings—VIII-8-21, ♂; VIII-2-48, ♀; VII-29-43, ♀; VII-27-43, ♀; VII-17-44, ♂; VII-12-66, ♀; VII-15-66, ♀; VII-19-66, ♀; VI-?-67, 2 ♂♂; VII-26-68, ♂; VII-24-68, ♂; VII-29-68, ♂; 2 ♂♂, no dates; Volga—2 ♂♂, 4 ♀♀, no dates.

Catocala amestris Strecker (1 specimen): Sioux Falls—VII-12-78, ♀.

Catocala coccinata Grote (1 specimen): Sioux Falls—VII-9-78, ♀.

Catocala ultromia (Hübner) (20 specimens): Brookings—VII-21-79, ♂; VII-27-22, ♂; VII-30-38, ♀; VII-19-43, ♂; VII-25-43, ♂; VIII-2-43, ♀; VII-20-44, ♀; VII-12-48, ♂; VIII-6-65, ♂; VII-26-66, ♂; VIII-23-68, ♂; Sioux Falls—VIII-3-78, ♀; VIII-5-78, ♂; VIII-3-79, ♂, ♀; VII-9-79, ♀; VIII-18-79, ♀; Volga—♂, 2 ♀♀, no dates.

Catocala blandula Hulst (1 specimen): Brookings—VII-16-66, ♂.

Catocala mira Grote (21 specimens): Sioux Falls—VI-30-77, ♀; VII-9-78, ♂; VII-11-78, 2 ♀♀; VII-12-78, ♂, ♀; VII-14-79, ♂; VII-15-79, 2 ♂♂; VII-16-79, ♂; VII-19-79, ♂; VII-23-79, ♂; VII-24-79, 2 ♀♀; VII-26-79, 3 ♂♂, ♀; VII-28-79, ♀; VII-30-79, ♂, ♀.

Catocala grynea (Cramer) (34 specimens): Brookings—VIII-12-42, ♂; VII-25-43, 3 ♂♂; VII-27-43, ♂; VIII-2-43, 2 ♂♂; VIII-10-43, ♂; VII-20-44, ♂; VIII-8-44, 2 ♂♂; IX-

TABLE 1. Comparison of three collecting methods used for *Catocala* in Sioux Falls from 1976–1979.

Species	Light		Bait		Resting site	
	Male	Female	Male	Female	Male	Female
innubens			3	3		
insolabilis			1	2		
palaeogama			1	1		
neogama			5	4		
ilia			1	3		
cerogama		1	1	1		
parta		1	35	26	1	
meskei			5	2		1
luciana	1		5	2	1	
cara			2			
amatrix			2	2		
nuptialis	1	2	1			
amestris				1		
coccinata				1		
ultromia		1	2	3		
mira	2	1	10	7		
grynea	1	1	9	7	1	1
clintonii			1			
minuta	4	1	4	7		
amica				1		
Totals	9	9	88	73	3	2
Totals (male & female)	18		161		5	

14-44, ♂; VII-30-68, ♂; VIII-6-68, ♂; Sioux Falls—VII-7-77, 2 ♀♀; VIII-2-77, ♂; VII-4-78, ♂; VII-11-78, ♀; VII-12-78, 2 ♂♂, ♀; VII-22-79, 2 ♂♂; VII-24-79, ♀; VII-27-79, ♂; VII-28-79, ♀; VII-30-79, ♂; VIII-3-79, ♂; VIII-4-79, ♂, ♀; VIII-20-79, ♀; VIII-21-79, ♂; IX-5-79, ♀; Volga—reported as common (Truman, 1896), no specimens.

Catocala clintonii Grote (1 specimen): Sioux Falls—VII-12-78, ♂; Volga—reported as rare (Truman, 1897), no specimens.

Catocala minuta W. H. Edwards (16 specimens): Sioux Falls—VII-3-76, 2 ♂♂; VII-8-78, ♂, ♀; VII-9-78, ♂, ♀; VII-12-78, ♂, 4 ♀♀; VII-15-79, ♂; VII-23-79, ♂; VII-24-79, ♀; VII-30-79, ♀; VIII-5-79, ♂.

Catocala amica (Hübner) (2 specimens): Brookings—VII-26-79, ♂; Sioux Falls—VIII-3-78, ♀.

In the S.D.S.U. collection is a specimen of *G. aholibah* Strecker with the label "South Dakota" in Truman's handwriting. This is probably a Californian specimen. Truman is known to have placed South Dakota labels on some Californian material.

DISCUSSION

In comparing the collecting methods used in this study, by far the most successful was the use of bait. A total of 161 specimens were collected at bait representing 88 males and 73 females (Table 1). This contrasts with only 18 specimens collected at light and five at resting sites. Only *C. nuptialis* and *C. minuta* had greater than 25% of specimens collected at light. Of the 63 *C. parta* collected, only two were

TABLE 2. Flight periods of *Catocala* in eastern South Dakota and southern New England.

Species	Eastern South Dakota	Southern New England
	Flight period	
innubens	VII-7 to VIII-28	VII-31 to IX-20
neogama	VII-22 to VIII-31	VII-19 to X-14
parta	VI-23 to VIII-21	VII-29 to X-14
luciana	VII-23 to IX-1	—
meskei	VII-4 to VIII-21	—
whitneyi	VI-? to VIII-8	—
ultromia	VII-12 to VIII-18	VII-11 to IX-28
mira	VI-30 to VII-30	VII-22 to VIII-28
grynea	VII-4 to IX-14	VII-12 to IX-8
minuta	VII-3 to VIII-5	—

not at bait. The data show that no collecting method was more effective for one sex than another.

It is interesting to note the differences in species and numbers of specimens in one locality for the years 1978 and 1979. In 1978, 58 specimens and 18 species were collected. In 1979, 116 specimens and 14 species were collected. During the two years, collecting was in the same place (Sioux Falls, S.D.), using the same procedures, and collecting in the same time frame (2030 to 0200 hours). In 1979 *C. ilia, C. amestris, C. cerogama, C. coccinata, C. clintonii* and *C. amica* were not collected, while *C. insolabilis* and *C. palaeogama* were not seen in 1978. Of the 20 species 12 (60%) are common to both samples and eight (40%) are found in only one sample.

The unpredictability of bait has been well documented (Sargent, 1976). This was evident in our study in 1979. *Catocala* were found on every day in July when collecting was done, except on the 7th, and on all but five days in August (1, 7, 8, 10, 11). This contrasts with high *Catocala* counts for other dates (July 19, 20, 22, 24).

Differences in flight periods between *Catocala* of eastern South Dakota and southern New England have been found (Table 2). The New England data are from Sargent (1976). *C. innubens* records begin three weeks later in New England than in South Dakota. *C. parta* records for South Dakota begin a month before their New England counterparts. *C. mira* flies three weeks earlier in S.D. (there are no *C. erataegi* records and only one *C. blandula* record for S.D.).

The flight period of *C. grynea* begins earlier and ends later in South Dakota. This is interesting as New England records are based on many more specimens. *C. grynea* collected from Sioux Falls present an interesting pattern with regard to specimen conditions and dates.
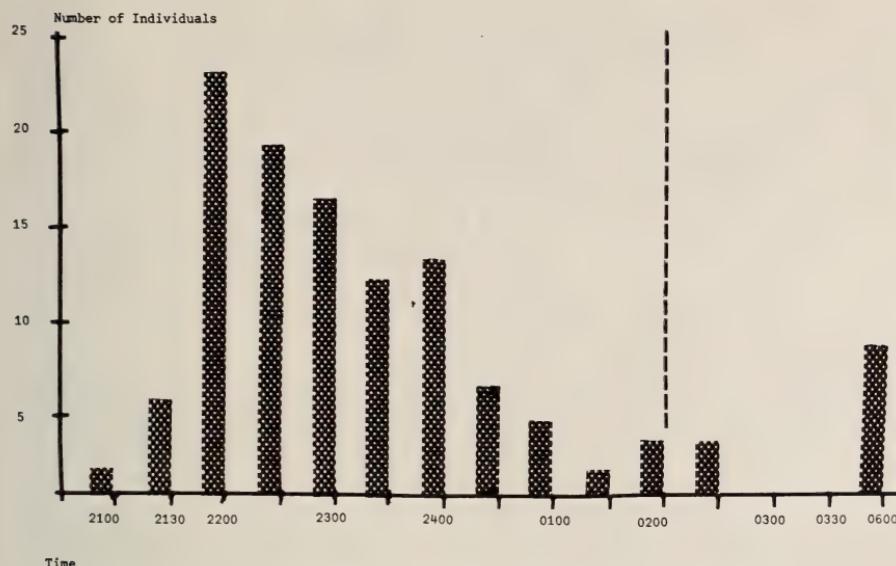
FIG. 1.   Flight times versus numbers of *Catocala* for Sioux Falls, 1979.
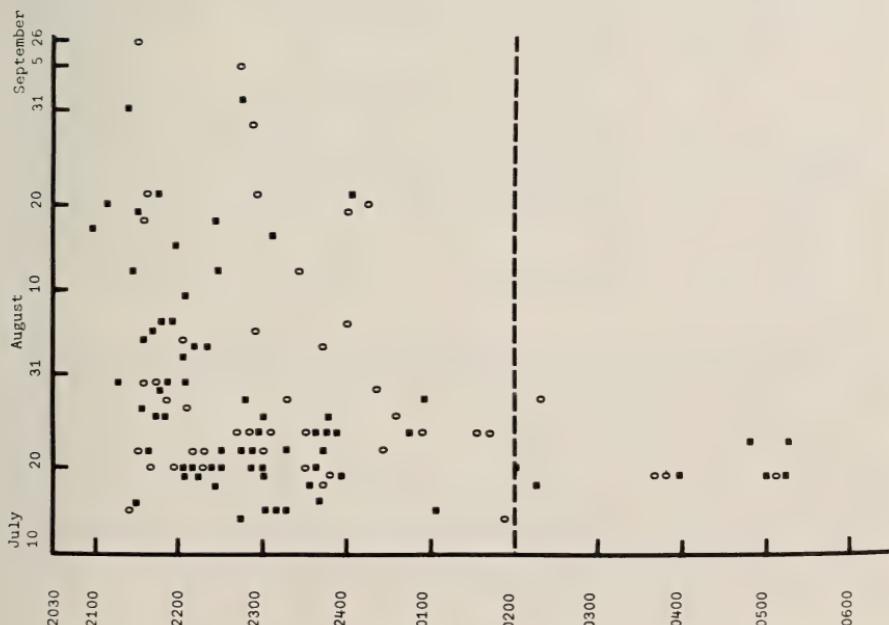
FIG. 2.   Flight times broken down by sex for *Catocala* in Sioux Falls, 1979—filled squares represent males; open circles represent females.

Specimens collected from 22 July to 4 August range from perfectly fresh ones to weathered individuals by 4 August. Specimens collected on 20, 21 August and 5 September are again perfect. However, 1978 data do not show such a pattern. More information is needed to determine whether there is a partial second brood or delayed emergence of *C. grynea* in eastern South Dakota.

The greatest period of *Catocala* activity in Sioux Falls was between 2130 and 2400 hours (Fig. 1). The light and baited trees were checked twice weekly for periods after 0200 hours, and one night a week collecting was continued until dawn. Both light and bait were checked continuously from 2100 to 0200 hours.

Comparing *Catocala* flight periods and sex ratios reveals interesting patterns (Fig. 2). It was seen that the majority of males were active before 2400 hours, while females tended to show a more even flight pattern. As the season progressed flight times tended to start and end sooner. Before 31 July there were 11 records between 2400 and 0200 hours. After 31 July there were only three records, and after the 31st no records after 0200 hours.

Literature Cited

Forbes, W. T. M. 1954. Lepidoptera of New York and Neighboring States. III. Noctuidae. Cornell Univ. Ag. Expt. Sta., Mem. 329. 433 pp.

McDunnough, J. 1938. Checklist of the Lepidoptera of Canada and the United States of America. Part 1. Macrolepidoptera. Mem. So. Calif. Acad. Sci. Vol. 1. 275 pp.

Sargent, T. D. 1976. Legion of Night. The Underwing Moths. Univ. of Mass. Press, Amherst. 222 pp.

Smith, John B. 1891. List of Lepidoptera of Boreal America. Am. Ent. Soc., Philadelphia. 124 pp.

Truman, P. C. 1896. Lepidoptera in South Dakota. Ent. News 7: 298–299.

——— 1897. Lepidoptera in South Dakota. Ent. News 8: 27–29.

A NEW SPECIES OF *AUTOMERIS* HÜBNER (SATURNIIDAE) FROM THE MISSISSIPPI RIVER DELTA

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ABSTRACT. A new species, closely related to *Automeris io* (F.), is described in both adult and larval stages. It is unusual in its loss of sexual and seasonal dimorphism, salt-marsh habitat, and brownish coloring, which appears to be a cryptic adaptation to the grassland environment.

On the open, treeless, salt marsh or cordgrass prairie of the outer Mississippi River delta there occurs a population of an *Automeris* species that differs markedly in coloring from *A. io* (F.) and from all other members of this complex. Although clearly derived from a recent *io* ancestor and probably indistinguishable structurally, the new taxon differs in reduction or near loss of sexual dimorphism, a characteristic of the *io* group. It has also lost the seasonal dimorphism of the contiguous *A. io lilith* (Strecker) of drier inland habitats. There appears to be an abrupt boundary between the two forms, with no sign of overlap or intergradation. Such evidence suggests that the delta form is a distinct species. The North American species of *Automeris* were comprehensively treated by the senior author (Ferguson, 1972) and by Lemaire (1971–74), but this taxon was at that time still uncollected.

Automeris louisiana Ferguson and Brou, **new species**
Figs. 2–6

Male (Figs. 2–4). Similar in basic pattern to *A. io lilith* (Fig. 1), but lines of upperside of forewing and underside of both wings usually evanescent. Antemedial line of forewing lacking entirely in about half the specimens; postmedial line and row of submarginal spots beyond it weak and diffuse. Upperside pattern of hindwing as in *io*. Underside with postmedial lines present but relatively weak. Discal spots normal. Most conspicuous distinguishing feature is the uniform, slightly olivaceous, light tan-brown coloring of the forewings, body, and entire underside. Coloring resembles that of *Automeris cecrops pamina* (Neumögen) of New Mexico and Arizona. Ground color of males of *lilith* from Louisiana (Fig. 1), above and beneath, is bright yellow, variably suffused with pinkish or deep reddish brown, especially toward base of forewing, and
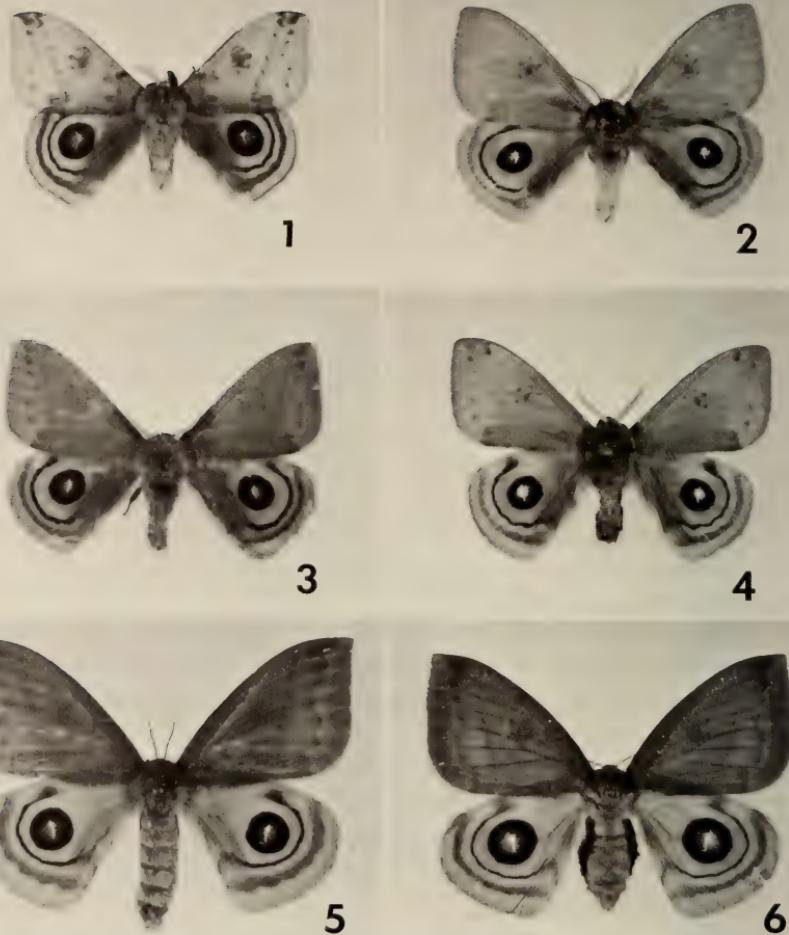
Figs. 1–6.   Louisiana specimens of *Automeris* species. **1.** *A. io lilith* ♂, Edgard, 23 Aug. 1973, V. A. Brou (normal Gulf Coast form of *io*). **2.** *A. louisiana,* n. sp., holotype. **3.** Same, paratype ♂, Golden Meadow, 26 Mar. 1975, V. A. Brou. **4.** Same, paratype ♂, Point au Fer Island, Terrebonne Parish, 22 June 1976, G. Adams. **5.** Same, allotype. **6.** Same, paratype ♀, Point au Fer Island, Terrebonne Parish, 18 Aug. 1975, G. Adams. All figures two-thirds actual size.

with body a lustrous, golden yellow. *A. louisiana* lacks all yellow coloring except that surrounding the ocellate discal spot on the hindwing, all other yellow being replaced by light tan that may or may not have a slightly olivaceous overlay. Discal spot of forewing (upperside) and the several dots surrounding it indicated in a darker shade, often diffuse; other markings of forewing usually indistinct. Hindwing with outer border brown instead of yellow (as it may also be in early spring specimens of *lilith*). Undersides of both wings same light-brown shade as upperside of forewing; discal spots normal; postmedial line of forewing reddish, of hindwing brown to purplish, both much weaker than those of *lilith*; forewing flushed with dull rose in median space

toward inner margin, but less extensively so than that of *lilith*. Fringes of both wings light brown, concolorous with wings, not contrastingly darker as is usually true of *io* subspecies. Length of forewing: holotype, 30 mm; other males, 26–31 mm. Average wing length 29.4 mm, about 7% greater than that of *io* from Louisiana.

Male genitalia probably indistinguishable from those of *io*. Three males dissected showed a tendency toward a simpler uncus, having two rather than the usual three transverse ribs, but no other consistent differences.

Female (Figs. 5, 6). Differs from that of *io* in having assumed nearly the same coloring as the male. Forewing light olivaceous brown, only slightly darker than that of the male, with usual markings indistinct or missing. Most prominent marking is the irregular, offset, submarginal line, showing as a line of contact between darker proximal and lighter distal zones. Hindwing and underside of both wings like those of male. The unicolorous dull brown of this species is in striking contrast to the deep purplish-red coloring of the forewings and thorax in females of *lilith*. Length of forewing: allotype, 41 mm; other females, 37–41 mm. Average wing length 39.1 mm, about 4.5% greater than that of *io* from Louisiana.

Types. Holotype ♂ (Fig. 2), Golden Meadow, Lafourche Parish, Louisiana, 20 June 1975, at light, V. A. Brou; Type No. 76,457, U.S. National Museum of Natural History. Allotype ♀ (Fig. 5), Venice, Plaquemines Parish, Louisiana, 30 March 1977, G. Adams. Paratypes: 5 ♂♂, Golden Meadow, Lafourche Parish, 28 February, 26 March, 1 May, and 18 June 1975, V. A. Brou; 8 ♂♂, 1 ♀, same locality, 14 March 1980, at UV light, V. A. Brou; 1 ♂, Cocodrie, Terrebonne Parish, 7 April 1975, G. Adams; 1 ♂, 1 ♀, Point au Fer Island, Terrebonne Parish, 18 August 1975, G. Adams; 1 ♂, 1 ♀, same locality and collector, 22 June 1976; 1 ♂, Leeville, Lafourche Parish, 26 March 1976, same collector; 2 ♂♂, Venice, Plaquemines Parish, 29 March 1977, same collector; 5 ♂♂, 1 ♀, same locality and collector, 30 March 1977. Added to the paratype series also are 50 ♂♂ and 50 ♀♀ reared in June 1980 from the female taken at Golden Meadow, 14 March 1980. All localities cited are in Louisiana. Holotype and allotype deposited in U.S. National Museum of Natural History; paratypes in U.S. National Museum of Natural History, American Museum of Natural History, Canadian National Collection, Los Angeles County Museum of Natural History, British Museum (Natural History), London, Muséum National d'Histoire Naturelle, Paris, and collections of Louisiana State University at Baton Rouge, V. A. Brou and G. G. Adams.

Early stages. Over 200 larvae of *A. louisiana* were reared by the junior author and by Gary Adams in the spring of 1980, mostly from a female collected at Golden Meadow on 14 March. A few larvae of *A. io* from a nearby locality in Louisiana were reared at the same time for comparison. Eggs of *louisiana* laid 15–18 March hatched in 2–2½ weeks; the larvae fed from about 1 April to 15 May, and adults emerged 14–16 days later. This is based on part of the brood reared (by Adams) at nearly normal outdoor conditions of temperature and humidity and is thought to closely approximate the natural developmental period. Others reared indoors in an air conditioned building took 2–3 weeks longer.

The larva is similar to that of *io* but appears to differ in two obvious features, the width and length of the bicolored lateral stripe, and the general body coloring of the fourth instar. A comparison of colored photographs of *louisiana* larvae with about 16 preserved, sufficiently unfaded, last-instar examples of *io* (including one from New Orleans) in the U.S. National Museum revealed that in the new species the red spiracular band is much wider than the white subspiracular band, nearly encroaching upon the bases of the dorsolateral tubercles. Consequently the spiracles, instead of being situated at the upper edge of the red band as is usual in *io*, are in the middle of it. The white subspiracular stripe tends to be about twice as wide as in *io*. Another difference is that the red and white lateral bands begin on the third thoracic segment in *A. louisiana*, on the first abdominal segment in *io*. With respect to the general coloring of the larvae, it was noted (by Brou) that this changes from brown to green an instar later in *louisiana*. Fourth instar larvae of *io* are green while those of *louisiana* are still brown, or yellowish brown. The larval spines, like those of *io*, can cause a severe stinging sensation if touched.

The larvae accepted and did well on live oak (*Quercus virginiana* P. Mill.), wild black cherry (*Prunus serotina* Ehrh.), and a species of plum (*Prunus* sp.) and were reared mainly on the black cherry. Newly hatched larvae fed on eastern cottonwood (*Populus deltoides* Bartr.) but only poorly; later instars refused it. Of these plants, only a low, stunted, shrubby form of live oak grows in the marshland habitat where it could be a natural host. Other oaks may be present but this has not been established. The food plant of *A. louisiana* in nature remains unknown. The ability to adapt to herbaceous plants or even grasses has not been uncommon in the Hemileucinae, and *H. io* is known to feed on a wide variety of such plants, including cultivated cotton and corn. *Pseudautomeris grammivora* (Jones) is a grass feeder on *Rottboellia compressa* L. in Argentina (Bourquin, 1945: 22). Inasmuch as live oak occurs widely in adjacent areas of the Gulf States where *A. louisiana* is not found, it would seem that this moth may have some special marsh food plant that has not yet been identified.

Habitat. The marshland habitat of *A. louisiana* is classified by Küchler (1964: legend item 78) as Southern Cordgrass Prairie. About 3500 square miles (5600 square kilometers) of the Mississippi River delta are occupied by this wet grassland. It continues westward along the Louisiana coast and as a narrower, more interrupted band all the way along the Texas coast to the Mexican border. The dominant plant is smooth cordgrass, *Spartina alterniflora* Loisel. Other main components of the vegetation are *Carex* spp., *Distichlis spicata* (L.) Greene, *Juncus effusus* L., *J. roemerianus* Scheele, *Mariscus* sp., *Panicum* spp., *Phragmites communis* Trin., *Sagittaria* spp., *Scirpus* spp., other *Spartina* spp., *Typha domingensis* Pers., and *Zizaniopsis miliacea* (Michx.) Doell & Aschers (Küchler, 1964).

REMARKS

This curious and unexpected species, although obviously a close relative of *Automeris io,* is unusual in having nearly lost the sexual dimorphism characteristic of its group. *A. io* and its Mexican relatives that have been available for examination, namely *hebe* (Walker), *melmon* Dyar, *dandemon* Dyar, *colenon* Dyar, and *thyreon* Dyar, are consistent in maintaining highly developed color differences between males and females. Only *A. eogena* (C. & R. Felder), also from Mexico, agrees in having lost the dimorphism, but the genitalia (figured by Lemaire, 1973: fig. 199) show it to be a distinct species. *A. louisiana* also lacks the seasonal polymorphism characteristic of the geographically adjacent taxon, *A. io lilith*; adults of *louisiana* flying in February and March are similar to those of the second brood in June or of the third brood in August. *A. io* subspecies *lilith* and *neomexicana* Barnes & Benjamin may have brownish males in the spring brood, but the females, with their deep purplish-red forewings, are always extremely different. *A. louisiana* averages 2–3 mm larger in wing length than *io* from nearby areas, measured against specimens from seasonally corresponding generations. As in so many marsh and grassland Lepidoptera, the coloring appears to be a cryptic adaptation related to habitat, the species having assumed the color of dead grass on all surfaces normally exposed in a resting posture.

Some information on the hours of flight is available but probably not enough to be used to show whether the new species differs from *io* in this respect. Notes kept by Adams indicate that the peak flight

activity may occur one to one and one-half hours before sunrise, based on 47 males and 6 females observed in one night at an offshore oil rig near Venice, Plaquemines Parish in March 1977. In March 1980, the junior author collected 3 females within one hour after sunset and 10 males between 1 and 2 hours after sunset, but lights were not operated after midnight.

Automeris louisiana was discovered in 1975 when the junior author collected several specimens at the lights of a food processing plant at the town of Golden Meadow, on Bayou Lafourche. Golden Meadow is on a narrow strip of land surrounded by salt marshes. Other specimens were collected that same year and in 1977 by Gary G. Adams at oil rig lights in the marshes in Lafourche, Plaquemines and Terrebonne Parishes, some of these sites being accessible only by boat or air and situated several miles from the nearest trees.

Literature Cited

Bourquin, Fernando. 1945. Mariposas Argentinas. 212 pp., 192 figs., 3 maps. Published by the author, Buenos Aires.

Ferguson, D. C., *in* Dominick, R. B. et al. 1972. The Moths of America North of Mexico, fasc. 20.2B, Bombycoidea, Saturniidae (in part), pp. 155–275, pls. 12–22.

Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. American Geog. Soc. Spec. Publ. 36, map and manual, 39 + 110 pp., illus.

Lemaire, Claude. 1971–74. Révision du Genre Automeris Hübner et des Genres voisins. Biogéographie, Éthologie, Morphologie, Taxonomie (Lep. Attacidae). Mém. Mus. Natl. Hist. Natur., Nouv. Série, Série A, Tome 68, pp. 1–232, pls. 1–29 (Part 1, 1971); Tome 79, pp. 233–422, pls. 30–49 (Part 2, 1973); Tome 92, pp. 423–576, pls. 50–61 (Part 3, 1974).

OBSERVATIONS ON THE ECOLOGY OF *EUPLOEA CORE CORINNA* (NYMPHALIDAE) WITH SPECIAL REFERENCE TO AN OVERWINTERING POPULATION

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ABSTRACT.   A study of a sub-tropical overwintering aggregation of the common crow butterfly, *Euploea core corinna* (Nymphalidae: Danainae), has been made on the campus of Griffith University, Brisbane, Australia. Observations on the temporal and spatial phenology of the aggregation, together with the sex ratio, reproductive status, individual fat content and physical condition of butterflies within the aggregation are presented. The aggregation was restricted to the upper reaches of a gully on the campus between mid-May and late July. Physical conditions in the gully (temperature, humidity and wind) were less severe than in adjacent areas. The butterflies in the gully were reproductively inactive. We suggest that such aggregations, apart from avoiding severe winter conditions, may also serve as mating concourses at the end of the winter season.

The common crow butterfly, *Euploea core* (Cramer), is widely distributed in the Indo-Australian region and is represented in Australia by the subspecies, *corinna* (W. S. Macleay) (Fig. 1). Recent general accounts of its life history are given by McCubbin (1971) and Common & Waterhouse (1972). These authors summarize information on foodplants, phenology, behavior and morphology, principally collated from the observations of field naturalists. McCubbin (1971) alluded to the formation of overwintering aggregations of this species in sheltered coastal sites and offshore islands in the tropics and subtropics of northern and eastern Australia.

Winter aggregations are also recorded for a variety of Australian danaines including *E. sylvester* (F) and *E. tulliolus* (F), *D. hamatus* (W. S. Macleay) and *D. affinis* (F). They are restricted to the period May–September, the dry season (Leeper, 1970) in north-eastern Australia, when temperatures remain above freezing for the most part (but see the discussion below).

The discovery of an aggregation of *Euploea core corinna* on the campus of Griffith University, Brisbane, Queensland in May 1979, prompted our observations on the population biology of the butterfly. These observations were continued from May to September although the aggregation had largely dispersed by early July. The results of these studies are presented in the present paper. In addition, we have taken the opportunity to speculate on the role and evolution of overwintering behavior of this type.

Our observations included estimates of the size of the overwinter-

ing population, its sex ratio, physical condition and the fat content of samples of individuals. The reproductive status of female butterflies was also examined. These studies, together with environmental measurements and behavioral observations provide a systematic basis for further research.

MATERIALS AND METHODS

The Study Area

The overwintering aggregation was centered in a gully which forms the upper section of the Rocky Waterholes Creek catchment adjacent to the Griffith University forest study area (27°33′E, 153°05′S) some 10 km S of Brisbane, Queensland. A general description of the area is given by Birk (1979). The topography of the site is shown in Fig. 3. The vegetation comprised relatively open mixed eucalypt forest with an overstory dominated by *Angophora woodsiana* F. M. Bailey, *Casuarina littoralis* Salisb., *Eucalyptus baileyana* F. Muell. and *E. umbra* R. T. Bak (Fig. 2). There were also many standing dead trees, notably *Casuarina*, in the area, especially along the lower sides of the gully. The understory comprised a variety of woody shrubs including *Pultenaea villosa* Willd., *Alphitona excelsa* (Fenzl.) Benth., *Acacia cunninghami* Hook., *A. aulocarpa* A. Cunn. ex Benth. and *Xanthorrhoea johnsonii* R. Br. A sparse and varied herb layer of grasses and forbs was present.

The approximate boundaries of the overwintering aggregation are indicated on the map (Fig. 3). Essentially, the overwintering insects occurred along the floor and lower sides of the gully, concentrating in the upper, deeper area to the north. The lower end of the concentration was ill-defined and one or two insects could be stirred up along much of the length of the gully floor throughout the period of observation.

Environmental Monitoring

During much of the study, continuous records of shade temperatures and relative humidity were collected at two locations within the study area. These are indicated in Fig. 3 and were chosen to permit microclimatic characterization of the overwintering site itself and the adjacent forest. These observations were made using two thermohydrographs maintained in screened boxes at ground level. A maximum and minimum thermometer accompanying each instrument permitted weekly calibration of the records of temperature. Information on prevailing wind directions was collected from records for Brisbane city made available by the Bureau of Meteorology.
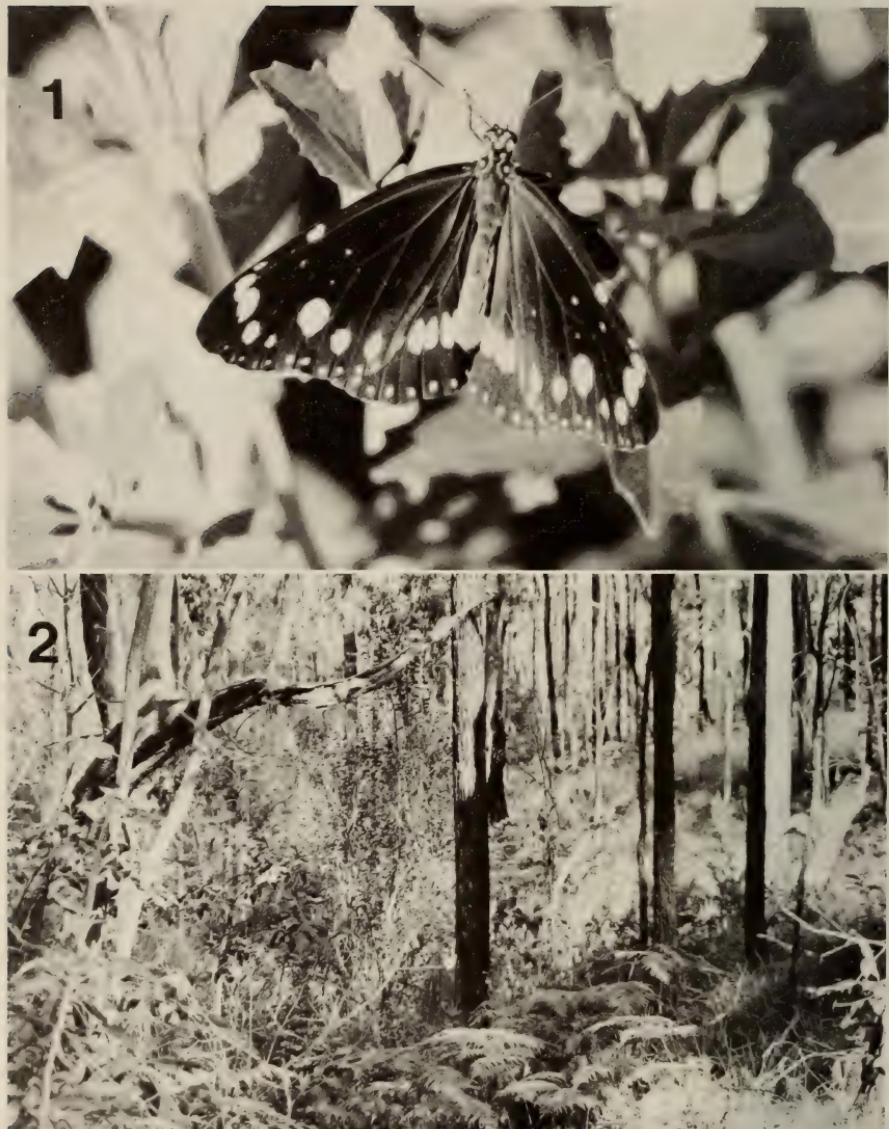
FIG. 1. Adult of *Euploea core*.
FIG. 2. General view of overwintering site.

Population Parameters

The population of butterflies was sampled on eight occasions from 4 June to 11 July 1979 with an additional post-winter sample taken in September. On each occasion two collectors spent 15–20 min netting adults which were temporarily caged in darkened boxes. They were subsequently tagged using the method of Urquhart (1960), em-
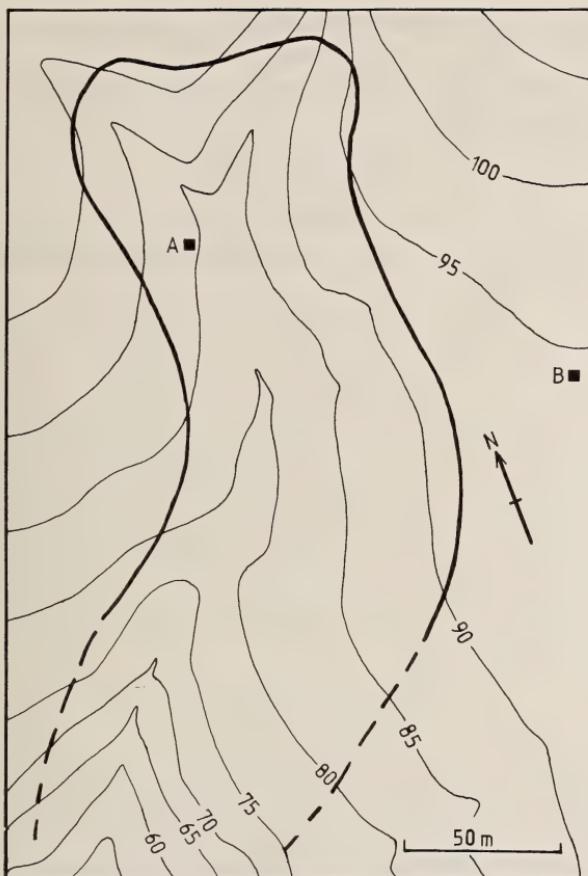
FIG. 3. Contour map of the upper catchment of Rocky Water Holes Creek, Brisbane, Queensland indicating the meteorological monitoring sites (A and B) and the approximate boundaries of the overwintering colony of *Euploea core corinna* (indicated by the heavy line).

ploying self-adhesive, individually numbered labels. These were affixed to the forewings of the insects by folding them over the costal margin after rubbing the scales off this region of the wing. Sex and wing condition of the captured butterflies were noted. A three point scale was adopted to categorize wing condition, *viz*, "intact" (perfect wing-margins), "chipped" (up to approximately 20 mm² of wing missing), and "very chipped" (more than 20 mm² of wing missing).

A subsample of males and females was removed for determination of fat content (see below) and the females were dissected to check whether they had mated (indicated by the presence or absence of spermatophores in the bursae copulatrices) and amount of ovarian development, if any.

The frequencies of recapture of marked insects in the first six sam-

ples were used to estimate the size of the colony by calculation of simple Lincoln indices. In addition, preliminary estimates of survivorship were obtained from the recapture data using the approach of Ehrlich & Gilbert (1973).

Fat Content

The subsamples of butterflies were returned, live, to the laboratory within 20 min of capture. They were killed and frozen immediately for later analysis (stored at $-12°C$).

In general, we used the technique of Tuskes & Brower (1978) to determine total fat content of the insects. The insects were first dried for 48 h at 50°C. They were weighed using a Mettler HR4AR balance and ground to a powder using a glass pestle and mortar. Using the method of Tuskes & Brower (1978), the powder was weighed and transferred to a glass vial to which was added 15 ml of a 2:1 chloroform/methanol mixture. The vials were sealed and agitated gently for 24 h. The solvent mixture was subsequently filtered off and evaporated to dryness in a preweighed glass tube. The reweighing of the tube, this time with the dry residue, permitted estimation of the gross lipid content for each insect.

Other Observations

On each sampling occasion we made notes on the behavior of the butterflies. In addition, we recorded occurrence of other species of butterflies and flowering plants available as nectar sources.

A sequence of oviposition observations by this species on plants of *Asclepias fruticosa* (L.) in an experimental plot 1.0 km from the overwintering site, was available from a long term population study of *Danaus plexippus* L. This provided a useful adjunct to the overwintering study, as did casual observations on the presence or absence of *E. c. corinna* adults elsewhere on the campus and adjacent areas.

Results

Environmental Monitoring

Table 1 summarizes the temperature and relative humidity readings taken in the gully and on the adjacent ridge from 15 June to 16 July 1979. These indicate that the gully provides a buffered environment relative to that of the adjacent ridge. Minimum temperature readings are consistently at least 2°C higher in the gully than on the ridge. The regression of ridge minimum temperatures on corresponding readings from the gully indicates that the differences between gully and ridge minima decrease as (gully) temperatures increase. Maximum daily

temperature readings are slightly lower in the gully, but are not significantly different from the ridge readings.

Relative humidity readings are consistently higher in the gully relative to the ridge both during the day and night. During the day the gully is a constant 5% more humid than the ridge over the range of readings (slope $\approx$ 1.0, intercept $\approx$ 5). At night the differences are smaller as overall humidity increases (slope > 1.0).

The gully is also sheltered by its N–S orientation from the influence of prevailing winds. Between May and August these are W to S–W in the mornings and S–E to N–E in the afternoons.

Population Parameters

Table 2 contains the results of the population studies and estimates of population parameters derived from them.

The estimates of density (x) and the associated standard deviations (s) given in columns 4 and 5 of the Table are derived by calculation of a simple Lincoln index on subsequent pairs of observation using the formulae:

$$x = \frac{an}{n}$$

and
$$s^2 = \frac{a^2 n(n-r)}{r^3}$$

where n is the total number of individuals in the second sample, a is the total number of marked individuals and r is the total number of recaptures (see Southwood, 1966, for further discussion of the method, its assumptions and drawbacks). The very small number of recaptures and consequent large variances demand that we discount the estimates for 7 and 27 June. The intervening figures, however, we feel reflect the actual size of the aggregation within the stated limits. In summary, there were 1200–1600 individuals in the aggregation during the winter period of study.

Throughout the study there was a preponderance of males (column 6 of Table 2) in our samples. The temporal variations in the sex ratio we ascribe to sampling error and suggest that the overall mean of our estimates of the ratio (2.16, s = 0.606) is the best estimate for the overwintering period as a whole. The sex-ratio in the spring sample was higher than most of the winter estimates but, again, this may be due to sampling error.

The condition of the butterflies using the criteria outlined above, is summarized in columns 7, 8 and 9 of Table 1. Throughout June, the condition of insects sampled was good with more than 90% of

Table 1. Summary of temperature and relative humidity data collecting in the overwintering site ("gully") and an adjacent area ("ridge"). Standard deviations are given in parentheses.

Datum	No. of observations	Gully	Ridge	Regression of ridge (R) on gully (G)	R value
Mean minimum temp. (°C)	27	9.6 (2.67)*	7.9 (2.87)*	$R_{min} = 1.06G_{min} - 2.31$	0.9862
Mean maximum temp. (°C)	28	21.4 (1.73)NS	21.8 (1.88)NS	$R_{max} = 0.85G_{max} + 3.71$	0.7935
Temp. range (°C)	—	7–24	5–25	—	—
Mean night RH (%)	26	89.5 (2.5)**	82.8 (4.2)**	$R_{nig} = 1.43G_{nig} - 45.0$	0.8293
Mean day RH (%)	28	51.0 (11.1)*	44.0 (11.2)*	$R_{day} = 0.98G_{day} - 4.96$	0.9583
RH range	—	34–98	27–90	—	—

**, *, NS: Indicates level of significance of difference (P < 0.001; P < 0.05, not significant).

Table 2. Population parameters of the subject population of *Euploea core corinna*. KEY: x indicates a mean estimate, s, its standard deviation and n the number of observations. See text for further explanation.

Sampling dates (1979)	Total captured	No. of marks	Lincoln Index estimate x	Lincoln Index estimate s	males / females	Condition (%)[1] I	Condition (%)[1] C	Condition (%)[1] VC	Females mated (%)	Development	Fat content (%) x	Fat content (%) s	Fat content (%) n
Winter													
4 June	48	—	—	—	1.29	27	71	2	0	None	24.3	3.46	7
7 June	47	1	2256	2232	3.27	36	59	5	0	None	—	—	—
12 June	47	4	1116	534	2.13	30	68	2	0	None	—	—	11
15 June	66	6	1562	608	1.87	27	69	4	0	None	21.0	3.86	11
22 June	37	5	1539	640	2.70	30	65	5	0	None	—	—	—
27 June	37	2	4532	3117	2.27	15	84	1	0	None	—	—	—
6 July	6	—	—	—	2.00 }	29	53	18	0	None	17.9	3.25	11
11 July	11	—	—	—	1.75 }				0	None			
Spring													
9–15 September, 1979	17	—	—	—	3.25	46	29	25	100	Advanced	18.3	2.96	4

[1] I = "intact"; C = "chipped"; VC = "very chipped."

captures in "intact" or "chipped" condition. The proportion of "very chipped" individuals rose sharply in the final winter sample (11 July) and showed a further increase in the spring sample.

The samples of females dissected during the winter period were all non-mated with no apparent ovarian development. This was in sharp contrast to the spring sample, in which all females examined were mated and had recognizable ova in their ovarioles.

The "longevity" of adult butterflies in the gully can be estimated from known minimum ages of recaptured insects. Table 3 summarizes this information and is based on animals marked between 4 and 27 June. The number of recaptures, 22 out of 282 released, is low and makes the survivorship estimates at best a first approximation. These life-span estimates are better considered as residence times in the marked population and as such are compounded of daily mortality and movements up and down the gully. Males have a longer mean "life-span" in the gully relative to that of the females (11.2 vs. 7.9 days). These differences are not due to sampling bias as the proportion of male to female recaptures (13:7) is similar to our estimates for the overall population (2:1). Neither is the difference due to differences in mortality, as the following four individuals indicate. Female number 50 was marked on 7 June and recaptured on 7 September in the gully. This individual was in "chipped" condition when first marked and had, presumably, been alive for some time before being marked. She was "very chipped" when recaptured. Female 96 was marked on 12 June in "intact" condition and was recaptured on 3 September outside the gully area (760 m to the E) in "chipped" condition. Male number 293 was intact when marked on 14 September and "chipped" when recaptured 980 m E of the gully on 11 October. Male number 91 was marked on 12 June and recaptured 122 days later, 3 km SSE of the campus. All of these butterflies had further expectation of life if wing condition is taken as an indicator of age. This is particularly true of female 96, which on dissection revealed early egg development and, presumably, would have had the bulk of her reproductive life ahead of her. *E. core* is therefore capable of living as long as 160 days if we take 80 days as a conservative estimate of the mean life expectancy (females 50 and 96 lived an average of 87 days at least). The difference in male/female residence times in the gully can be attributed to differences in vagility; females being more likely to move up and down the gully than males, and hence less prone to recapture in the limited netting area.

Fat Content

Results from analyses for total fat content are presented in columns 12–14 of Table 2. They indicate a steady and significant decline in

TABLE 3. Longevity of marked *Euploea core corinna* in the overwintering aggregation. (See text for further comment.)

Minimum no. of days surviving	Males	Females	Total
3	—	2	2
5	1	1	2
7	2	—	2
8	3	1	4
10	3	1	4
11	1	1	2
15	1	1	2
20	1	—	1
26	1	—	1
Total	13	7	20
Mean minimum life-span (MMLS)[1]	11.2	7.9	10.0
% daily survival (S)[2]	91.1	87.3	90.0

[1] MMLS = Σ min days survived × number surviving/Total number recaptured (Ehrlich & Gilbert, 1973).
[2] S = 1/1 − MMLS (Edmunds, 1969).

the fat content of the overwintering butterflies from 24.3% on 4 June to 17.9% on 11 July. Results for males and females did not differ significantly and, hence, the estimates given combine figures for both sexes. The fat content of the spring sample showed an increase over that of the last winter sample although this was not significant, and was probably due to the small sample size of the spring insects.

Other Observations

During the overwintering period a number of persistent behavior patterns were observed in the adult insects. Most insects spend the greater proportion of their time at rest on the vegetation at levels from about 1 m to 6 m from the ground. They were particularly numerous on the branches of standing dead *Casuarina* trees. When undisturbed and during sunny periods several desultory flights of a few meters could be observed at any time. When disturbed, however, large numbers of insects would fly up and down the gully at about head height. No substantial lateral movements were observed. Such flights were frequently in apparently coordinated groups with up to a dozen or more insects moving in unison. These drifts were of both sexes, but were not mating flights and no mating behavior was seen in the period of overwintering. This correlates with the unmated status of dissected females (see above).

Very few other butterflies were observed in the gully at the same time as *E. core*, although several *Danaus chrysippus petilia* were seen, apparently passing through the area. A few resident *Melanitis leda* (Satyrinae) were present in the gully but their characteristic low
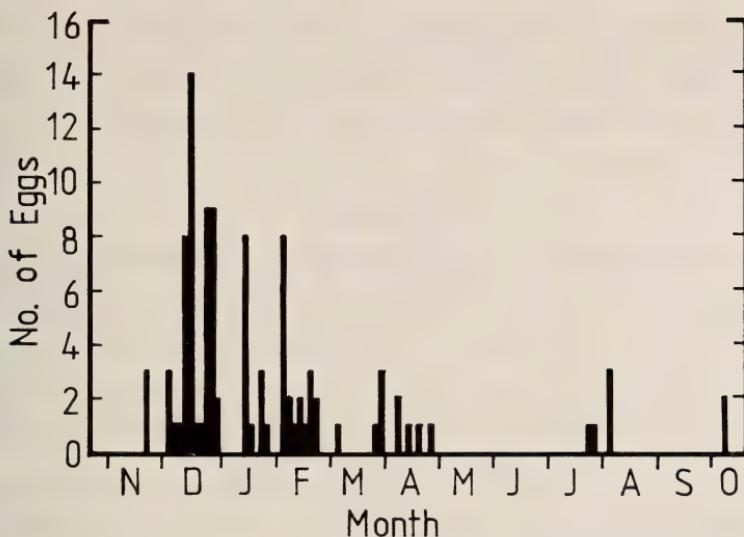
FIG. 4. Histogram of numbers of eggs of *Euploea core corinna* laid on *Asclepias* plants from November 1977 to October 1978.

vagility and ground dwelling habit excluded any but the most minor interaction with *E. core*.

During the overwintering period the only obvious nectar sources in the gully were a few flowers of the weed *Ageratum houstonianum* Mill. At the end of the period of observation, however, when the aggregation was dispersing, a variety of species were in flower including *Gomophlobium latifolium* Sm., *Leptospermum flavescens* Sm., and *Xanthorrhoea johnsonii*, on all of which *E. core* was observed to feed. Many other herbs and shrubs also begin to flower in the sclerophyll forest at this season.

A comparable period of overwintering was also defined, albeit circumstantially, in the observations on oviposition phenology of *E. core* made in a prepared plot of *Asclepias* spp. These results are for the previous winter (November 1977 to October 1978) and are presented as Fig. 4. Not only do these data support our observations concerning the temporal and spatial integrity of the overwintering aggregation, they are also the first records of the phenology of egg-laying in the species. The spatial integrity of the aggregation was evidenced largely by the total absence of sightings of the butterfly in areas adjacent to the gully in the period, early June to early July 1979. Subsequently butterflies, several of which bore our labels, were observed regularly in areas of the campus away from the gully. One such insect was retrieved in September, 3 km from the site of the gully. After the

breakup of the overwintering aggregation, mating and ovipositing activity began, although insects remained in the gully. Oviposition on campus took place on leaves of the vine, *Parsonsia straminea*, on which larvae were subsequently reared successfully.

Discussion

In any consideration of overwintering in adult butterflies, the reference point must be the extensive work on the phenomenon in North American *Danaus plexippus*. Key classical and recent works on the species in this context include Urquhart (1960, 1965), Urquhart & Urquhart (1976), Brower et al. (1977), Tuskes & Brower (1978) and Calvert et al. (1979). In Australia such aggregations of *D. plexippus* have been reported, briefly, by Smithers (1965).

Euploea core in Australia, unlike *D. plexippus* in North America, is not migratory although it does show occasional extensions in range southwards in favorable seasons (see, for example, Kitching et al., 1978). The existence of overwintering aggregations in parts of its range, then, represent contractions in its distribution in response to unfavorable seasonal conditions and not the end-points of some regular directional mass movement. Such contractions of range are recorded for *D. plexippus* in Australia by Smithers (1977) although these result in restricted winter breeding areas. They also occur on a continental scale whereas *E. core* appears to be concentrated in, at most, a regional scale. The overwintering swarms of *D. plexippus* that have been observed in Australia are not, as far as is known, associated with any regular migrations and occur in early winter adjacent to breeding ranges (Smithers, 1965).

That the aggregations observed in *E. core* are in areas of more equable climate than elsewhere in their environs is evidenced by the climatic data presented in this paper. The few degrees amelioration in minimum temperatures experienced in the gully would be sufficient to permit its inhabitants to avoid the occasional light frosts occurring during most winters in this subtropical region. In addition, the region is one of summer rainfall with little or no fresh vegetation growth during the period when the overwintering aggregations occur. The clustering behavior, thus, can be regarded partly as a further response to the lack of food, both for larvae and imagines, which Wolda (1978) uses to account for the marked seasonality he observed in various neotropical phytophagous insects.

We suggest that the butterflies are in a largely quiescent stage during the period of aggregation and evidence for this is derived from closer examination of the data on fat content. Following Gibo & Pal-

lett (1979) it is possible to use the metabolic data of Zebe (1954) to examine the energetic demands of butterflies in terms of their wet weights. These authors suggest a basal metabolic rate for butterflies (based initially on data from *Vanessa* sp.) of 2 cal/g/h. If we calculate the energetic demands of butterflies of the mean wet weight of our samples of *E. core* between 4 and 15 June we arrive at a figure of 99.8 cal or, taking the caloric equivalent of fat to be 9.09 cal/mg (Weiss-Fogh, 1970), an equivalent weight of 11.0 mg of fat. This compares favorably with our estimate of the loss of fat over that period (12.1 mg) suggesting for this period that the insects were indeed quiescent, living off their reserves of fat. A similar calculation for the period 15 June to 11 July produces an expected fat loss of 31 mg which is considerably more than the observed 12.2 mg decline. This suggests that some food intake occurred during this latter period and, indeed, the observed coincidence of the time of breakup with the appearance of a variety of floral nectar sources lends support to the idea that nectar feeding begins at and, indeed, may trigger the end of the overwintering aggregation.

Calvert et al. (1979) report considerable predation on clustered *D. plexippus* by birds, notably orioles and grosbeaks. Evidence of predation on *E. core* was rare. One individual with an obvious beak mark was taken and a few wings were found on the gully floor, possibly evidence of spider predation. Of the local birds the pied butcher bird, *Cracticus nigrogularis* Gould, a generalist predator, was noted in the gully and is a likely candidate as predator of the butterflies. Bowers & Wiernasz (1979) have defined particular types of wing damage in the satyrine, *Cercyonis pegala,* which they attribute to avian predation. Their categories include triangular tears, straight tears across major veins and symmetrical damage to opposite or ipsilateral wings. Although we noted the extent of wing-chipping in *E. core* throughout the period of study, damage of the type indicated by these authors was not observed and such wing-tearing as was noted seems much more likely to be the result of contact with vegetation and other physical wear and tear than of encounters with predators. We conclude that in the period for which we have data predation was not high.

From an evolutionary point of view the question, "why form overwintering aggregations?" is of interest. Butterflies may overwinter in any one of their life history stages and, even in the same region, different groups exhibit different strategies. That the danaines are so apt to exhibit what is perhaps the least common road, and overwinter as adults, frequently in aggregations such as that described here for *E. core* requires some further consideration. Tuskes & Brower (1978) observed that during the latter part of overwintering aggregations of

D. plexippus, mass mating flights occur. Although no mating was observed in our studies, the high proportion (100%) of mated females in our September sample and the higher proportion of "very chipped" insects in our later samples provides, in our view, strong circumstantial evidence that mating in this species is coincident with the period of breakup of the overwintering aggregation. This, with Tuskes & Browers' (1978) observations, leads to the suggestion that such aggregations may serve as mating concourses, adding to the variety of the mechanisms described by Shields (1967) and Scott (1968, 1974), among others, by which butterflies overcome the mate-finding problem so acute in animals with widely dispersed oviposition sites.

The observations presented here leave a number of fascinating questions unanswered. Foremost among these are matters pertaining to the mode of formation of overwintering groups such as the one described here. Do late summer emergents actively seek out an overwintering site or are they "captured" by the site, as it were, when passing through? Given the propensity for these and other butterflies to use gullies as natural flyways, the latter mechanism seems most likely. This then raises questions about the role of such sites in the dynamics of the local population. To what extent are such sites "traditional"? Even allowing for the exceptional longevity of the species, the individuals which enter the overwintering site will be at least one generation removed from those that dispersed from such sites the previous spring. How many sites are there in a given area and how does this relate to the movement potential of the species? These and other questions must await results of further investigation now in progress.

Literature Cited

Birk, E. M. 1979. Disappearance of overstorey and understorey litter in an open eucalypt forest. Aust. J. Ecol. 4: 207–222.
Bowers, M. D. & D. C. Wiernasz. 1979. Avian predation on the palatable butterfly, *Cercyonis pegala* (Satyridae). Ecol. Ent. 4: 205–209.
Brower, L. P., W. H. Calvert, L. E. Hendrick & J. Christian. 1977. Biological observations on an over-wintering colony of monarch butterflies (*Danaus plexippus*, Danaidae) in Mexico. J. Lepid. Soc. 31: 232–242.
Calvert, W. H., L. E. Hedrick & L. P. Brower. 1979. Mortality of the monarch butterfly (*Danaus plexippus* L.): avian predation at five overwintering sites in Mexico. Science 204: 847–851.

COMMON, I. F. B. & D. F. WATERHOUSE. 1972. Butterflies of Australia. Angus & Robertson, Sydney. 497 pp.

EDMUNDS, E. 1969. Polymorphism in the mimetic butterfly *Hypolimnas misippus* L., in Ghana. Heredity 24: 281–302.

EHRLICH, P. R. & L. E. GILBERT. 1973. Population structure and dynamics of the tropical butterfly, *Heliconius ethilla*. Biotropica 5: 69–82.

GIBO, D. L. & M. J. PALLETT. 1979. Soaring flight of monarch butterflies, *Danaus plexippus* (Lepidoptera: Danaidae), during the late summer migration in southern Ontario. Can. J. Zool. 57: 1393–1401.

KITCHING, R. L., E. D. EDWARDS, D. FERGUSON, M. B. FLETCHER & J. M. WALKER. 1978. Butterflies of the Australian Capital Territory. J. Aust. Entomol. Soc., 17: 125–133.

LEEPER, G. W. (ed.). 1970. The Australian Environment. 4th ed. CSIRO/Melbourne University Press, Melbourne. 163 pp.

McCUBBIN, C. 1971. Australian Butterflies. Nelson, Melbourne, Sydney. 206 pp.

SCOTT, J. A. 1968. Hilltopping as a mating mechanism to aid the survival of low density species. J. Res. Lepid. 7: 191–204.

——— 1974. Mate-locating behaviour of butterflies. Amer. Midl. Nat. 91: 103–117.

SHIELDS, O. 1967. Hilltopping. J. Res. Lepid. 6: 69–178.

SMITHERS, C. N. 1965. A note on overwintering in *Danaus plexippus* (Linnaeus) (Lepidoptera, Nymphalidae) in Australia. Aust. Zool. 13: 135–136.

——— 1977. Seasonal distribution and breeding status of *Danaus plexippus* (L) (Lepidoptera: Nymphalidae) in Australia. J. Aust. Ent. Soc. 16: 175–184.

SOUTHWOOD, T. R. E. 1966. Ecological methods with special reference to the study of insect populations. Methuen, London. 391 pp.

TUSKES, P. M. & L. P. BROWER. 1978. Overwintering ecology of the monarch butterfly, *Danaus plexippus* L., in California. Ecol. Ent. 3: 141–153.

URQUHART, F. A. 1960. The Monarch Butterfly. University of Toronto Press, Toronto. 361 pp.

——— 1965. A population study of a hibernal roosting colony of the monarch butterfly (*D. plexippus*) in northern California. J. Res. Lepid. 4: 221–226.

——— & N. R. URQUHART. 1978. Autumnal migration routes of the eastern population of the monarch butterfly (*Danaus p. plexippus* L.; Danaidae; Lepidoptera) in North America to the overwintering site in the neovolcanic plateau of Mexico. Can. J. Zool. 56: 1759–1764.

WEISS-FOGH, T. 1970. Metabolism and weight economy in migrating animals, particularly birds and insects. In J. W. L. Beament & J. E. Trehern, eds., Insects and Physiology. Oliver & Boyd, London. pp. 143–159.

WOLDA, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. J. Anim. Ecol. 47: 369–381.

ZEBE, E. 1954. Uber den Stoffwechsel der Lepidopteren. Z. Vergl. Physiol. 36: 290–317.

HISTORICAL AND BIOLOGICAL OBSERVATIONS OF LEPIDOPTERA CAPTURED BY AMBUSH BUGS (HEMIPTERA)

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ABSTRACT.   Ambush bug predation on Lepidoptera represents a unique inverte-brate predator/prey relationship. Since its first description more than 100 years ago, it has been infrequently studied and reported. Observations on predator's sex and method of capture are presented along with a summary of lepidopteran families utilized as prey.

In a recent note Pyle (1973) reported what he believed to be the first account of ambush bugs (Phymatidae) preying on North American Lepidoptera. Subsequently, Fales (1976) added 14 observations and suggested that this phenomenon may occur more frequently than realized. I have made several field observations of invertebrate predators preying on Lepidoptera and have taken special interest in this behavior. I present here the first photographic account of an ambush bug/lepidopteran encounter, plus a summary of captures that have appeared in the entomological literature over the past century.

On 16 June 1979 at the St. Charles of Borromeo Seminary in Overbrook, Pennsylvania, I witnessed a capture involving *Wallengrenia egeremet* (Scudder) (Hesperiidae) and two ambush bugs, *Phymata fasciata* (Gray), on an inflorescence of *Apocynum cannabium* L. (Apocyanaceae). The butterfly was busily nectaring at inflorescences that are occupied by ambush bugs at this time of year. Suddenly, in an instant, the butterfly was pulled downward into the inflorescence. Closer examination revealed that two coupled ambush bugs were piercing and probing the butterfly's ventral surface while the latter's wings continued to beat rapidly and convulsively. Within two minutes the butterfly was subdued, most likely by the predators' toxins which probably were placed in strategic ventral ganglia. The coupled ambush bugs then proceeded to feed on the butterfly's haemolymph for the next 160 min with the large female manipulating and rotating the prey. After 90 min of feeding, the smaller male (8 mm) ceased to feed and rested on the female's dorsum (Fig. 1) while the female (10 mm) continued to feed for another 70 min before dropping the drained remains of the butterfly to the ground. Shortly after the moment of capture the butterfly's proboscis was observed to be quite mutilated. The two galeae were separated and twisted. This damage was prob-

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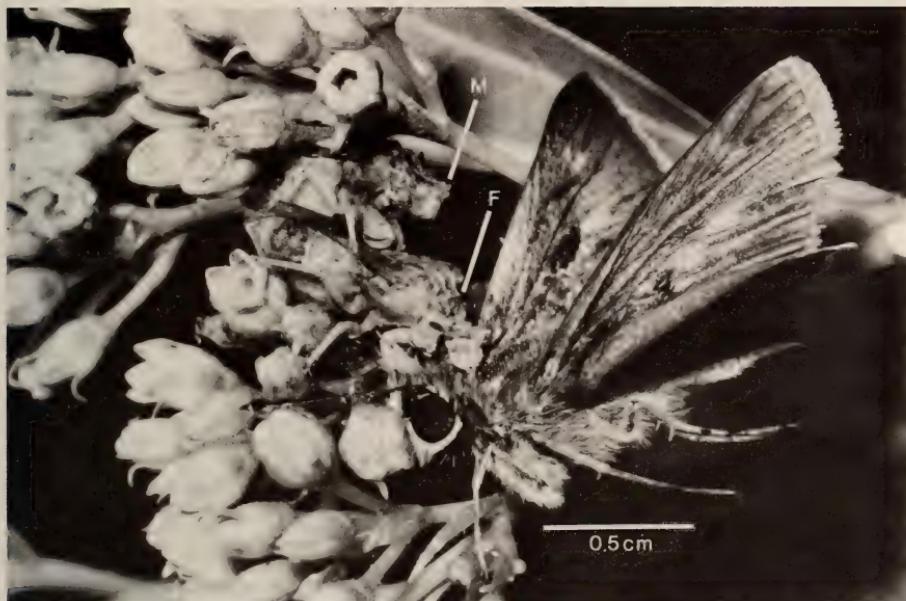
FIG. 1. *Wallengrenia egeremet* captured by two ambush bugs, *Phymata fasciata*, at Overbrook, Pennsylvania. The large female (F) is shown actively feeding on the prey, while the smaller male (M) has ceased to feed but remains coupled to the female.

ably inflicted when the ambush bug seized the proboscis and gave a violent jerk to draw the prey near. Balduf (1939) repeatedly observed that butterflies and moths were most often seized near the apex of their extended proboscis.

Butterflies ambushed by more than one bug have been previously reported (Pyle, 1973; Fales, 1976) but the details of the predators' sex were lacking. The term "coupled" as used in this report is not synonymous with copulation. It was coined by Balduf (1939) to describe the physical relationship of a pair of ambush bugs in which the male rests or perches passively on the dorsum of the female. During the courting season the male ambush bug frequently occupies this position for several hours or even days. He will also join in the feast when the larger, more active female has caught a prey. Thus at certain times of the year, it is not unusual to see more than one ambush bug feeding on a single prey. In general, when males are single they capture smaller insects, e.g., dipterans. For proper determination of sex, a small hand lens or dissecting microscope is necessary. Males may be distinguished by the elongated, rounded external covering of the genitalia, while the female genitalia is covered by a triangular flap-like shield.

The first report of ambush bugs preying on Lepidoptera appeared

TABLE 1. Summary of records of Lepidoptera captured by ambush bugs (Hemiptera: Phymatidae).

Family	Number of species	Number of individuals
Noctuidae	10	30
Hesperiidae	10	27
Pieridae	4	19
Nymphalidae	4	13
Lycaenidae	3	8
Ctenuchidae	1	4
Pyralidae	1	1
Total	33	102

more than 100 years ago (Glover, 1876). Near the old Maryland Agricultural College, Glover witnessed an ambush bug concealed among the petals of a rose, "busily employed in sucking out the juices of a small blue butterfly which it had caught and killed." Glover's "small blue butterfly" undoubtedly was one of the two common Plebejinae of Maryland, either *Celastrina argiolus pseudargiolus* (Bdv. & LeC.) or *Everes comyntas* (Godart); however, insufficient detail is presented to make a species determination. The first correct identification of a lepidopteran prey was made by Prof. J. A. Lintner (1878), former New York State Entomologist, from a specimen sent to him by Mr. G. W. Duvall of Annapolis, Maryland. The butterfly victim had been ambushed on goldenrod (*Solidago* sp.) and was determined by Lintner to be *Chrysophanus americana* D'Urban (=American Copper, *Lycaena phlaeas americana* Harris). I have attempted to catalogue (available from author upon request) all the lepidopteran captures by ambush bugs recorded in the literature during the past century since the first report (Glover, 1876; Lintner, 1878; Barnard, 1879; Riley, 1883; Adams, 1915; Balduf, 1939, 1940; Pyle, 1973; Fales, 1976; Neck, 1977; Nielsen, 1977). A summary of this catalogue presented in Table 1 shows that 102 individual captures have been recorded, distributed among 7 lepidopteran families and 33 species. All identified prey had been captured by members of the genus *Phymata*. To date, there are no recorded captures by the other phymatid genus *Macrocephalus*. Although these data do not provide a clear analysis of the bionomics of this unique predator/prey relationship, they do provide an interesting estimate of its overall distribution among different lepidopteran families. Noctuids and hesperiids constitute the majority of recorded prey and it is a little surprising that noctuids were the single most frequently recorded family. The Noctuidae are generally regarded as having nocturnal habits and it is easy to over-

look the diurnal and crepuscular habits of some of its members. Willis and Burkill (1895, 1903a, 1903b) recorded nearly 40 species of British moths visiting flowers in the daytime; in certain locales they recorded a greater number of visitations by noctuids and geometrids than all Rhopalocera combined. The pattern of lepidopteran feeding habits may vary from place to place and thorough predator records may be a useful tool in learning more about this important aspect of lepidopteran ecology.

Predation on Lepidoptera by ambush bugs, without doubt, occurs more frequently than the records summarized here would indicate. Balduf (1940) has shown in Illinois that Lepidoptera may constitute up to 20% of the total diet of a *Phymata* population over a season. I encourage lepidopterists to maintain a keen eye for this phenomenon, and would be most interested in learning of any further ambush bug/lepidopteran encounters.

LITERATURE CITED

ADAMS, C. C. 1915. An ecological study of prairie and forest invertebrates. Bull. Ill. State Lab. Nat. History 11: 174–175.

BALDUF, W. V. 1939. Food habits of *Phymata pennsylvanica americana* Melin (Hemiptera). Canad. Entomol. 71: 66–74.

——— 1940. More ambush bug prey records (Hemiptera). Bull. Brook. Entomol. Soc. 35: 161–169.

BARNARD, W. S. 1879. Meeting of the Entomological Club of the American Association for the Advancement of Science. Canad. Entomol. 11: 196.

FALES, J. H. 1976. More records of butterflies as prey for ambush bugs (Heteroptera). J. Lepid. Soc. 30: 147–149.

GLOVER, T. 1879. Manuscript notes from my journal or illustrations of insects, native and foreign, Order Hemiptera, suborder Heteroptera or plant-bugs. J. C. Entwisle, Washington, D.C., p. 57X.

LINTNER, J. A. 1878. An ugly bee-slayer. The Country Gentleman 43: 551.

NECK, R. W. 1977. Bizarre capture of a butterfly by an ambush bug. J. Lepid. Soc. 31: 22.

NIELSEN, M. C. 1977. Invertebrate predators of Michigan Lepidoptera. Great Lakes Entomol. 10: 113–118.

PYLE, R. M. 1973. *Boloria selene* (Nymphalidae) ambushed by a true bug (Heteroptera). J. Lepid. Soc. 27: 305–307.

RILEY, C. V. 1883. Report of the entomologist. Report of the Department of Agriculture for 1883. Washington, D.C. p. 113.

WILLIS, J. C. & I. H. BURKILL. 1895. Flowers and insects in Great Britain Part I. Ann. Bot. 9: 227–273.

——— 1903a. Flowers and insects in Great Britain Part II. Ann. Bot. 17: 313–349.

——— 1903b. Flowers and insects in Great Britain Part III. Ann. Bot. 17: 539–570.

PHENOTYPIC PLASTICITY IN TEMPERATE AND SUBARCTIC *NYMPHALIS ANTIOPA* (NYMPHALIDAE): EVIDENCE FOR ADAPTIVE CANALIZATION

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ABSTRACT. *Nymphalis antiopa hyperborea* from Fairbanks, Alaska failed to produce the aberrant phenotype "hygiaea" when subjected to cold-shock treatment which induces this phenotype in lowland California *antiopa*. This result is consistent with the hypothesis that canalization of the adult phenotype is an adaptive process.

The mourning cloak, *Nymphalis antiopa* L., has an enormous geographic range; it shows parallel N-S clines in the Palaearctic and Nearctic, but overall its phenotype is extraordinarily stable for a species which is not a regular migrant. Although it is double- or even triple-brooded southward, seasonal variation also seems to be nonexistent. Still, the phenotype of *N. antiopa*, like its close relatives, is very susceptible to modification by temperature shock applied to the pupa; many of the aberrations thus induced are very drastic, and some duplicate very rare wild-collected examples. This general picture of extreme geographic and seasonal stability coupled with extreme lability under experimental regimes applies to several species variously placed in the genera *Nymphalis, Aglais, Inachis, Vanessa,* and *Cynthia*. It was the object of much research between 1860 and 1940. Discussions of *antiopa* appear in Standfuss (1896) and Fischer (1907); the subject is reviewed analytically by Goldschmidt (1938). This last author, in 1935, coined the term "phenocopy" to describe mutant-like aberrations inducible by the imposition of stress during development. He explicitly recognized the similarity of such phenomena in *Drosophila* and in the Nymphalini.

In my laboratory we have been duplicating the classical European experiments, using Californian stock of common nymphalines as available. The exact procedures used by Fischer, Standfuss, Merrifield, and the other early writers are often incompletely described, so that differences in responses obtained from Californian and European stocks are difficult to evaluate. For the most part, the classical phenomena have been reproduced qualitatively and sometimes quantitatively. Comparisons among different Californian stocks are more easily controlled.

What—if any—is the evolutionary significance of these recurrent, aberrant phenotypes? This was a lively controversy in the heady, highly theoretical, intellectual climate of the late nineteenth century. A number of early writers considered them atavistic (reversional) to

an ancestral type, and some temperature-induced phenotypes of *N. antiopa* and *N. (=Inachis) io* L., the two species which depart most from the usual pattern in the genus, indeed betray "ancestral" elements. Shapiro (1976, 1979), following Standfuss & Merrifield (1894), attempted to relate the shock phenotypes of nymphalines to the seasonal polyphenisms of pierines and of the nymphalid *Araschnia levana* L.: the environmental sensitivity of the phenotype is viewed as an adaptive property of the genome ("canalization," Waddington, 1957) and a product of selection. The present paper reports an experimental test of this idea.

Experimental Protocol and Results

A named subspecies of *N. antiopa*, *hyperborea* Seitz, occurs in subarctic North America. It is characterized by small size, usually heavy dark markings in the yellow border, and a redder chestnut groundcolor. This subspecies is potentially subject in nature to cold shocks similar to those which produce shock phenotypes in Californian *antiopa* in the laboratory, although its seasonality minimizes the risk. I have found no records of aberrations taken in Alaska or the Yukon, while they do occur in California; this could easily be an artifact of the relative amount of collecting done in these areas. If, however, canalization were adaptive, one might expect that the phenotype of *hyperborea* would be better buffered against modification by low temperatures than that of Californian *antiopa*.

In 1979 six colonies of fourth-instar *antiopa* larvae, each uniform in age and presumed to originate from a single egg mass, were collected and used for cold-shock experiments. Four of these originated at sea level at Fairfield, California (38°15′N, 122°03′W), collected in May; the other two were from Fairbanks, Alaska (64°51′N, 147°43′W), collected in late June. All were taken from local *Salix* spp. and reared to pupation on *Ulmus procera* L. at 25°C in continuous light. Experimental animals were refrigerated 8 h after pupation and held for 2 weeks at 2°C before being returned to 25°C. Controls remained at 25° throughout. The results appear in Table 1.

Although the California colonies differed markedly among themselves, all gave at least one individual of the named aberration "hygiaea" (alive or dead) in the chilled groups. No hygiaea (Fig. 1) appeared among the Alaskan animals or in the California controls. We have never reared an hygiaea from an unchilled pupa, but we have obtained this striking aberration in 12 of the 13 California broods we have subjected to this treatment since 1973.

Temperature shock sufficient to induce aberrations usually kills a substantial number of the animals. To compensate for this, the ex-

Table 1. Results of temperature-shock experiments with *Nymphalis antiopa* from two localities (see text).

Brood, source	Normal live	Normal dead	Hygiaea live	Hygiaea dead	Unscor-able[1] dead	Totals[1]
Calif. no. 1 exptl.	30	1	1	0	12	44
control	15	2	0	0	0	17
						61
Calif. no. 2 exptl.	31	9	10	6	10	66
control	10	0	0	0	0	10
						76
Calif. no. 3 exptl.	25	5	5	8	12	55
control	8	0	0	0	1	9
						64
Calif. no. 4 exptl.	17	8	0	1	6	32
control	10	0	0	0	0	10
						42
Total California exptl.	103	23	16	15	40	197
control	43	2	0	0	1	46
					Total Calif.	243
Alaska no. 1 exptl.	29	3	0	0	11	43
control	10	0	0	0	0	10
						53
Alaska no. 2 exptl.	15	6	0	0	4	25
control	6	0	0	0	1	7
						32
Total Alaska exptl.	44	9	0	0	15	68
control	16	0	0	0	1	17
					Total Alaska	85
			Total animals raised: 328			

[1] Excluding individuals parasitized by Tachinidae.

perimental part of each colony was always much larger than the control. Most deaths occur after pigment has been laid down in the wings, so the phenotype can be scored. In any given brood the most extreme individuals generally die as pharate adults, or, if they eclose, are crippled, or unable to feed due to improper fusion of the proboscis. Exactly the same phenomena occur with heat-shock phenocopies in *Drosophila* (Mitchell & Lipps, 1978). There is still a residue of unscorable dead, always much higher in the chilled than the unchilled groups. Since these might have altered the phenotypic ratios had they developed further, a 2×2 contingency table was prepared for total scorable vs. unscorable in the two sets of colonies; the California and Alaska ratios were almost identical ($\chi^2 \sim 0.07$, $P > .750$), permitting
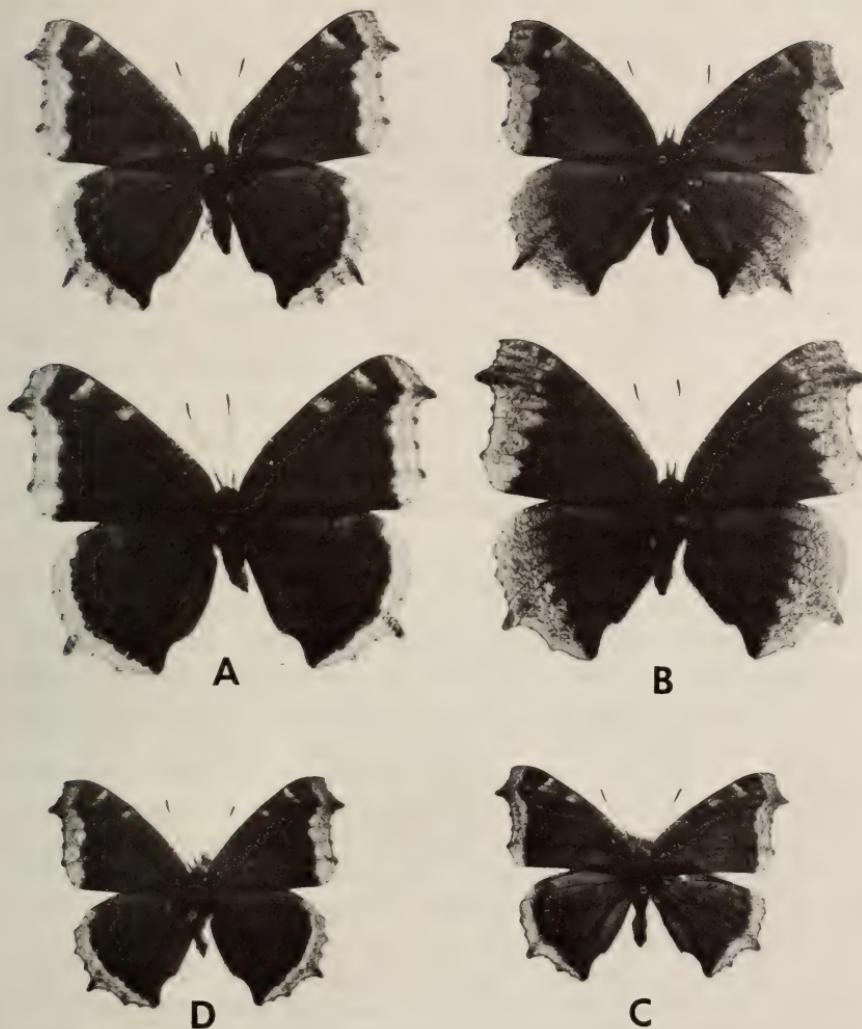
FIG. 1. Normal (A) and "hygiaea" (B) phenotypes of Fairfield, California *Nymphalis antiopa*, with normal chilled (C) and unchilled (D) *N. a. hyperborea* from Fairbanks, Alaska.

us to exclude the unscorables from the analysis. When total normal (alive + dead) vs. total hygiaea (alive + dead) are considered, the difference between California and Alaska is very highly significant ($\chi = 12.28$, $P \ll .005$): based on these samples Alaskan animals *are* better buffered against cold than Californian.

Discussion

This result is less convincing than appears at first glance, for three reasons. (1) The larval environment prior to collection was totally uncontrolled. Although there is no particular reason to think adult phenotype can be determined in this species by influences acting on the young larva, this possibility should be rigorously excluded. (2) The variability among the California colonies suggests that the hygiaea response is genetically variable. The adequacy of 4 California and 2 Alaska colonies as population samples is unknown. If only California broods 1 and 4 had been used in this experiment, the paper would not have been written! (3) Some modification of phenotype did occur in chilled Alaskan animals. The *hyperborea* phenotype is itself phenocopiable in California *antiopa* by temperature treatment (Shapiro, 1976), and chilled *hyperborea* respond by exaggeration of the subspecific characters, rather than by major changes in the pattern elements (Fig. 1).

The hygiaea phenotype is probably a phenocopy in the rigorous sense. In May 1979 one of more than 140 *antiopa* reared by A. P. Platt under outdoor Maryland conditions displayed this phenotype. The brood was from a female collected by P. Kean in Ann Arundel Co., Maryland (Platt, *pers. comm.*). Shapiro (1976; and unpublished) has found genetically-determined tendencies toward production of the elymi-muelleri-letcheri series of aberrations in *Vanessa annabella* Field in selected lines bred from wild aberrants. These facts underscore the notion that the difference between a simple "mutant" and a temperature-sensitive one is a modifier complex. In the case of nymphaline aberrations, the temperature-sensitive genes may be ubiquitous in many natural populations.

Shapiro's 1976 argument may be condensed as follows: in polyphenic species (pierines, *Araschnia levana*), alternate phenotypes are coupled to environmental factors which induce their expression *in those environments in which they are adaptive*. In species like *N. antiopa*, the normal phenotype is canalized over the entire range of probable environments, leaving plasticity to be expressed only under unnatural laboratory regimes. Since it is normally not expressed in nature, it is safe from selection; only the occasional individual expressing it under ecologically meaningful conditions is selected against.

To establish the plausibility of this argument, one needs to demonstrate that (1) the seasonal phenotypes of polyphenic species are adaptive in their respective seasons, and (2) the normal (canalized)

phenotype of monophenic species is adaptively superior to the shock phenotypes at all seasons. As usual, the pertinent data are difficult to obtain. The best evidence to date bearing on (1) is Watt's (1968, 1969) work on the thermoregulatory properties of the seasonal phenotypes of *Colias*. Even here, a purist might object that the inference of fitness advantage is unsupported by actual data on reproductive success. There are no direct data bearing on (2). Field tests will only be possible if a selected strain can be produced which reliably presents the aberrant phenotype under normal conditions, thereby circumventing the general weakness and inviability of temperature-shocked animals. The logic of the argument parallels current theory regarding the evolution of diapause and facultative sexuality.

A Multi-Level Approach

Recently Bowden (1979) severely criticized "the extreme selectionist position": "... visible characters appear not to be specially adapted to present local conditions." To some extent Bowden is demolishing a straw man; no one claims omnipotence for selection, and the role of history in limiting the variation available to be selected ("phylogenetic inertia") is generally, if grudgingly, acknowledged. The existence of such a controversy 120 years after Darwin is embarrassing, because rigorous and complete demonstrations of ecological causality in evolution are virtually non-existent. The evidence for adaptiveness is generally indirect. In Bowden's *Pieris napi* L. group, the parallels among seasonal, altitudinal, and latitudinal forms—all tending to be darker in colder or cloudier climates—point to thermoregulatory advantages of pattern. If it is objected that this does not rule out a fortuitous physiological effect of chilling during development—reflecting common ancestry rather than parallel selection—a mirror-image situation exists in South America, where similar melanin and pteridine phenotypes occur seasonally, altitudinally, and latitudinally in the endemic pierine genus *Tatochila*. Here the physiological control of the seasonal polyphenism differs from Holarctic systems, and there is a strong, if indirect, case for its convergent evolution from monophenic ancestors (Shapiro, 1980); convergence implies adaptive value.

Both variation and the *lack* of variation are potentially adaptive. Developmental geneticists working on *Drosophila* have now established that at least some phenocopies are related to temperature-stimulated synthesis of specific new proteins ("heat shock proteins") and cessation of normal protein synthesis in progress for a period after the application of stress (Mitchell, 1966; Tissières, Mitchell & Tracy,

1974; Mitchell & Lipps, 1978). If we assume that the cellular physiology of nymphaline phenocopies is not dissimilar, we have a new, more sophisticated framework in which to ask the old question about adaptiveness. We have a proposed cellular mechanism which could account for both seasonal and shock phenotypes. If they are evolutionarily related, it should account for these phenotypes. We know that in at least one phenocopy ("straw," Seybold, Meltzer & Mitchell, 1975) the same molecular control is at work in both mutant and shock examples. Waddington (1953) and Milkman (1963, 1966) proved the selectability of similar phenomena. The phenotypes and reproductive behavior of the nymphaline *Polygonia c-aureum* L. in Japan are under demonstrated neurohormonal control (Fukuda & Endo 1966; Endo, 1970, 1972). Such hormones may act by turning on and off the same genetic loci affected by temperature shock in our experiments.

Referring to its great stability, Bowden (loc. cit.) says: "How are the wing-markings of *Nymphalis antiopa* L. determined? Normalizing selection is working on ancestral genotypes, probably with no visible response to ecological conditions." Precisely, if the stress is on the work "visible." If the stable phenotype of *N. antiopa* is adaptively important, we would expect physiological adjustments to protect it in varying environments. Both polyphenism and monophenism are epiphenomena of a genetic control system, but that control system itself can evolve (Gould, 1977). Its evolution depends on the fitness of the phenotype it produces, which is what will be selected.

LITERATURE CITED

BOWDEN, S. R. 1979. Subspecific variation in butterflies: adaptation and dissected polymorphism in *Pieris* (*Artogeia*) (Pieridae). J. Lepid. Soc. 33: 77–111.
ENDO, K. 1970. Relation between ovarian maturation and activity of the corpora allata in seasonal forms of the butterfly, *Polygonia c-aureum* L. Devel., Growth & Differ. 11: 297–304.
——— 1972. Activation of the corpora allata in relation to ovarian maturation in the seasonal forms of the butterfly *Polygonia c-aureum* L. Ibid. 14: 263–274.
FISCHER, E. 1907. Zur Physiologie der Aberrationen- und Varietäten-Bildung der Schmetterlinge. Archiv für Rassen- und Gesellschafts-Biologie 4 (6): 761–793.
FUKUDA, S. & K. ENDO. 1966. Hormonal control of the development of seasonal forms in the butterfly *Polygonia c-aureum* L. Proc. Jap. Acad. 42: 1082–1087.

GOLDSCHMIDT, R. 1935. Gen und Aussereigenschaft (Untersuchungen an *Drosophila*). I–II. Z. Vererbungsl. 69: 38–69, 70–131.

——— 1938. Physiological Genetics. McGraw-Hill, New York. 375 pp.

GOULD, S. J. 1977. Ontogeny and Phylogeny. Harvard University Press, Cambridge, Mass. 501 pp.

MERRIFIELD, F. 1894. Temperature experiments in 1893 on several species of *Vanessa* and other Lepidoptera. Trans. Ent. Soc. London 1894: 425–438.

MILKMAN, R. 1963. On the mechanism of some temperature effects on *Drosophila*. J. Gen. Physiol. 46: 1151–1169.

——— 1966. Analyses of some temperature effects on *Drosophila* pupae. Biol. Bull. 131: 331–345.

MITCHELL, H. K. 1966. Phenol oxidases and *Drosophila* development. J. Insect Physiol. 12: 755–765.

MITCHELL, H. K. & L. S. LIPPS. 1978. Heat shock and phenocopy induction in *Drosophila*. Cell 15: 907–918.

SEYBOLD, W. D., P. S. MELTZER & H. K. MITCHELL. 1975. Phenol oxidase activation in *Drosophila*: a cascade of reactions. Biochem. Genet. 13: 85–108.

SHAPIRO, A. M. 1976. Seasonal polyphenism. Evol. Biol. 9: 259–333.

——— 1979. The evolutionary significance of redundancy and variability in phenotypic-induction mechanisms of Pierid butterflies (Lepidoptera). Psyche 85: 275–283.

——— 1980. Convergence in pierine polyphenisms (Lepidoptera). J. Nat. Hist. 14: 781–802.

STANDFUSS, M. 1896. Handbuch der palaärktischen Gross-Schmetterlinge für Forscher und Sammler. G. Fischer, Jena. 392 pp.

TISSIÈRES, A., H. K. MITCHELL & U. M. TRACY. 1974. Puffs and protein synthesis in *Drosophila*. J. Mol. Biol. 84: 389–398.

WADDINGTON, C. H. 1953. Genetic assimilation of an acquired character. Evolution 7: 118–126.

——— 1957. The Strategy of the Genes. Allen and Unwin, London. 262 pp.

WATT, W. B. 1968. Adaptive significance of pigment polymorphisms in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. Evolution 22: 437–458.

——— 1969. II. Thermoregulation and photoperiodically controlled melanin variation in *Colias eurytheme*. Proc. Nat. Acad. Sci. (USA) 63: 767–774.

AN *OXALIS* (OXALIDACEAE) FEEDING LARVA, *GALGULA PARTITA* (NOCTUIDAE)

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ABSTRACT. The ultimate instar larva of *Galgula partita* Guenée (Lepidoptera: Noctuidae) is described and illustrated. The hostplant for the larva of *G. partita* is documented as *Oxalis* (Oxalidaceae) which apparently is an unique larva/plant association among North American Lepidoptera.

This paper presents the first description of the ultimate instar larva of *Galgula partita* Guenée (Noctuidae: Amphipyrinae) and the first substantiated, published report of the larva's host. The detailed larval account may in time help establish the phylogenetic position of *Galgula* Guenée, which has no obvious relative, according to Forbes (1954), and is represented only by *partita* in Canada and the U.S.A. (McDunnough, 1938).

The only known larval host of *partita* is *Oxalis*. This statement is based on McFarland's (1965) indication, on the information in the description that follows, and on unpublished information at the U.S. National Museum of Natural History. Records from the latter source show that *Galgula partita* larvae were collected on *Oxalis* in Clemson, South Carolina, 15 December 1956 and were intercepted by USDA Plant Quarantine officials at Nogales, Arizona, 4 December 1960 and 4 August 1962 (Weisman, pers. comm.).

Associations of lepidopterous larvae feeding on species of Oxalidaceae apparently are rare. This is intriguing because there are seven genera and approximately 800 species in this plant family (Robertson, 1975). The situation may be related to the high concentration of oxalate in these plants. Details of the plants' chemistry were summarized by Hegnauer (1969), but additional speculation regarding possible plant resistance, etc., is beyond the scope of this paper. Basic larval hostplant indices and bibliographies (e.g., Forbes, 1954; Kimball, 1965; Kingsolver & Sanderson, 1967; Godfrey, unpubl. computerized host catalog) do not list any North American larvae of Lepidoptera from the Oxalidaceae. To my knowledge the only other published account of a lepidopteran being associated with an oxalid is McFarland's (1979) rearing of a geometrid, *Metallochlora militaris* (Lucas), on *Averrhoa carambola* L. (introduced plant) in Australia.

All line drawings in the following illustrations were done to scale, and explanation of the abbreviations was published previously (Godfrey, 1972).
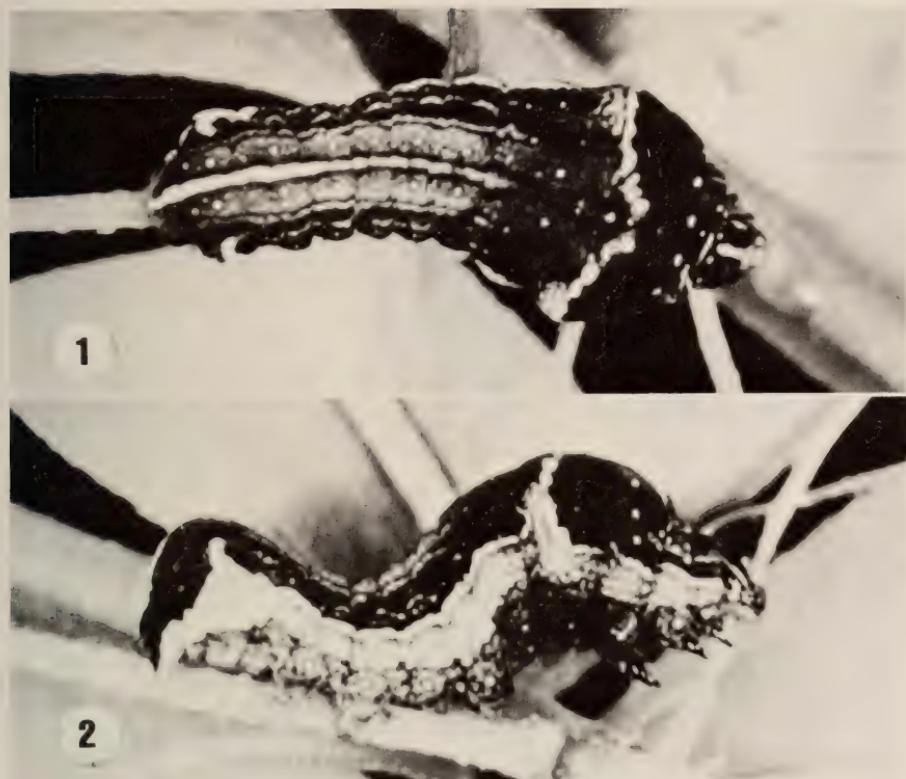
FIGS. 1–2. *Galgula partita:* **1,** dorsal view; **2,** lateral view (photographs by J. G. Franclemont).

Galgula partita Guenée

General. Head: integument smooth; width 1.40–1.50 mm ($\bar{x} = 1.47$). Total length 12–17 mm ($\bar{x} = 14.57$). **Body:** integument smooth; distinctly swollen at first abdominal segment (Ab1) (Fig. 1), abruptly tapering cephalad and slightly tapering caudad to Ab3; segments Ab4–7 of equal width, declivous from Ab8–Ab10 (Figs. 2, 9). All setae simple. Prolegs present on Ab3–6, 10; size increasing only slightly caudad on Ab3–6, those on Ab10 slightly smaller than on Ab6. Crochets mesoseric, uniordinal.

Head (Fig. 3). Postgenal sutures parallel to each other; length of epicranial suture 0.42–0.46 mm ($\bar{x} = 0.45$); height of frons (apex to Fa's 0.44–0.50 mm ($\bar{x} = 0.46$); distance F1–F1 0.28–0.34 mm ($\bar{x} = 0.30$); AFa cephalad and AF2 caudad of apex of frons; A1–3 forming right to slightly obtuse angle at A2; P1–P1 0.70–0.81 mm ($\bar{x} = 0.73$); P2–P2 0.84–0.91 mm ($\bar{x} = 0.87$); P1 insertion approximately midway between epicranial suture and L; L cephalad of juncture of adfrontal ecdysial lines; antennaria concave; Oc1–Oc2 0.03–0.04 mm ($\bar{x} = 0.03$); Oc2–Oc3 0.02–0.03 mm ($\bar{x} = 0.03$); Oc3–Oc4 0.03 mm ($\bar{x} = 0.03$).

Mouthparts. Hypopharyngeal complex (Fig. 4): spinneret elongate, tubular, its apex and tip of Lp2 extending subequally, length about 4.0 times length of Lpsl; length of Lpsl about 6.0 times that of stipular seta, 2.2 of Lpl, 10.0 of Lps2, 0.38 of Lp2; distal and proximal regions rather continuous; distal and proximomedial regions void of spines; proximolateral region bearing short, thin spines distally and about 12 flat, stout, lateral spines. **Mandible** (Figs. 5, 6): two outer setae present, distant from each other;
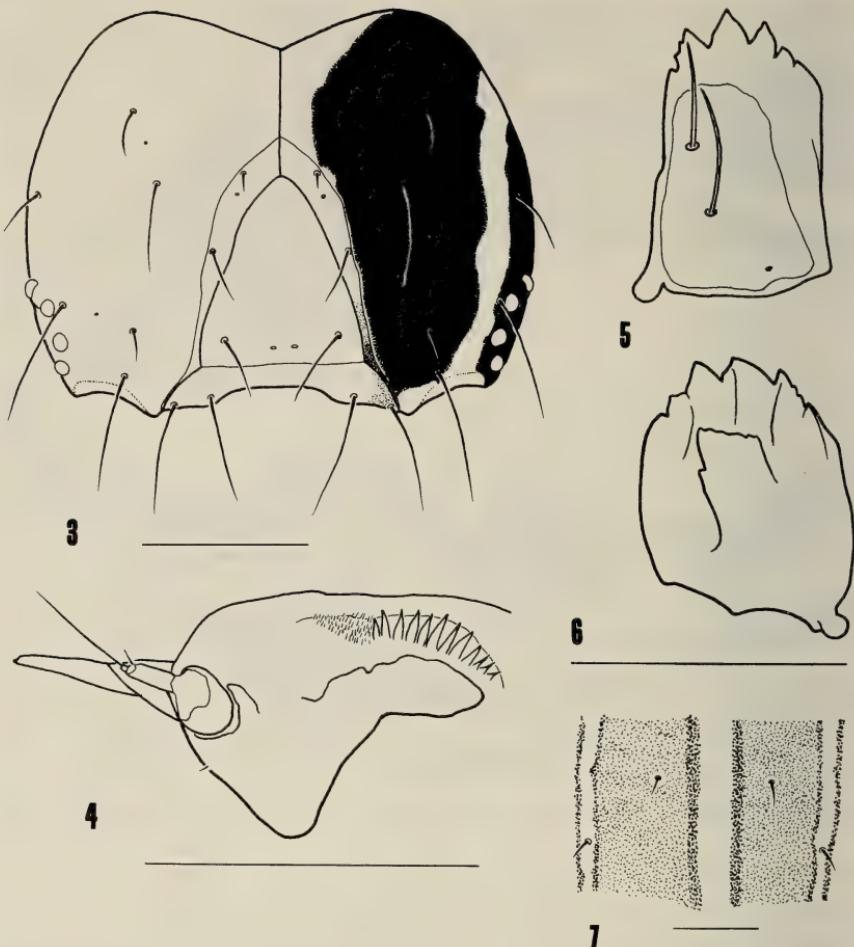
FIGS. 3–7. *Galgula partita*: **3,** head capsule, frontal view; **4,** hypopharyngeal complex, left lateral view; **5,** left mandible, outer surface; **6,** left mandible, oral surface; **7,** dorsum of seventh abdominal segment. Scale lines equal 0.5 mm.

inner ridges two and three terminating about at tips of outer teeth; inner tooth present, prominent, flat, longer than wide, sometimes broken and represented only by basal scar; first outer tooth small; second outer tooth serrated on side opposite first tooth; third and fourth teeth prominent, acutely angular; fifth tooth reduced but angular; sixth tooth reduced, rounded.

Thorax. Segment T1: SD1 & 2 setal insertions separated from edge of cervical shield (Fig. 8): interspace D1–D1 about 0.78 XD1–XD1; D2–SD2 about 1.53 SD2–XD2; setae SD1 and L2 present; spiracle elliptical, peritreme uniformly narrow. T2 (Fig. 8): D1–D2 about 1.0 D2–SD2; SD1 hairlike; coxal bases contiguous to narrowly separated; tarsal setae 1–3 slightly thickened, 4 merely setose; base of tarsal claw produced, rounded to obtusely angulate.

Abdomen. Segment Ab1: 2 SV setae. Ab2–6 with 3 SV setae, 1 on Ab 7 & 8. Dorsal and lateral chaetotaxy of Ab6–10 as in Fig. 9. Setae D2 set in white subdorsal lines on
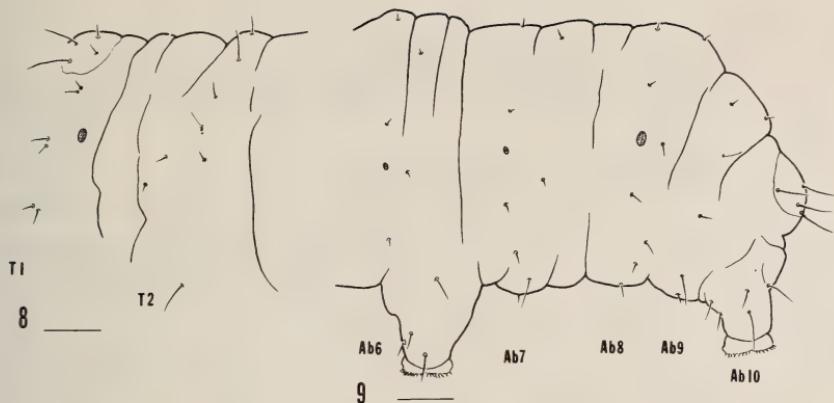
FIGS. 8–9. *Galgula partita:* **8,** dorsolateral chaetotaxy of prothoracic (T1) and mesothoracic (T2) segments; **9,** dorsolateral chaetotaxy of abdominal segments (Ab6–10). Scale lines equal 0.5 mm.

Ab2–7 (Fig. 7). Ab9: SD1 semi-hairlike, weaker than and distant from D1 and D2. Ab10: posterior margin of anal shield entire; dorsal surface of anal shield broadly convex; subanal setae merely setose, subequal to lateral setae of anal proleg. Height of spiracle on Ab7 0.08–0.11 mm ($\bar{x} = 0.09$), on Ab8 0.12–0.15 mm ($\bar{x} = 0.13$). Length of dorsal setae on Ab7 0.12–0.16 mm ($\bar{x} = 0.14$).

Coloration (living material). **Head** (Fig. 3): contrastingly marked, coronal and ocellar stripes glossy black, remainder of head essentially white or yellowish white; gular regions tinged with pink. **Body** (Figs. 1, 2): ground color brown; dorsal and subdorsal areas of T1–3 and subdorsal area of Ab1–9 dark brown; subdorsal area on Ab1–7 divided into dorsal and ventral stripes by thin, white line; dorsal area of Ab1–9 tannish brown; lateral area white with strands of tannish brown, continuous to tip of anal proleg; ventral area with strands of dark brown underlaid by white flecks; middorsal and subdorsal lines white, prominent on dark brown cervical shield, diffuse to absent on T2–Ab2; middorsal line of Ab3–10 white, continuous, becoming more distinct caudad; subdorsal lines on corresponding segments white and continuous but thinner, less distinct; dorsal margin of lateral area white, passing beneath spiracles on T1 and Ab1 then curving sharply dorsad on Ab1 and ending at D2, resuming at normal level at posterior margin of Ab1 and continuing caudad, running under but touching spiracles on Ab2 & 3 and passing above spiracles on Ab4–8, bending sharply dorsad on Ab8 to SD1. Spiracles dark brown to black with black peritremes. Thoracic legs black.

Material examined. 4 specimens: Highlands, Macon Co., North Carolina, August–September 1958, J. G. Franclemont, *Oxalis* sp. (yellow) (Franclemont collection). 3 specimens: IL.: Cook Co., University of Illinois Chicago Circle Campus, 16 August 1979; host—*Oxalis* sp. in greenhouse; coll. Larry Sykora (Illinois Natural History Survey collection).

LITERATURE CITED

CRUMB, S. E. 1956. The larvae of the Phalaenidae. U.S. Dept. Agr. Tech. Bull. 1135. 356 pp.

FORBES, W. T. M. 1954. Lepidoptera of New York and neighboring states. Pt. 3. Cornell Univ. Agr. Exp. Sta. Mem. 329. 433 pp.

GODFREY, G. L. 1972. A review and reclassification of larvae of the subfamily Had-eninae (Lepidoptera, Noctuidae) of America north of Mexico. U.S. Dept. Agr. Tech. Bull. 1450. 265 pp.

HEGNAUER, R. 1969. Chemotaxonomie der Planzen. Band 5. Dicotyledoneae: Mag-noliaceae-Quiinaceae. Basel & Stuttgart. 506 pp.

KIMBALL, C. P. 1965. The Lepidoptera of Florida: an annotated checklist. Arthropods of Florida and neighboring land areas. Vol. 1, 363 pp. Gainesville.

KINGSOLVER, J. M. & M. W. SANDERSON. 1967. A selected bibliography of insect-vascular plant associational studies. U.S. Dept. Agr., ARS 33-115. 33 pp.

MCDUNNOUGH, J. 1938. Check list of the Lepidoptera of Canada and the United States of America. So. Calif. Acad. Sci. Mem. 1(1): 1–275.

MCFARLAND, N. 1965. The moths (Macroheterocera) of a chaparral plant association in the Santa Monica Mountains of southern California. J. Res. Lep. 4: 43–74.

——— 1979. Annotated list of larval foodplant records for 280 species of Australian moths. J. Lepid. Soc., 33(3) Suppl. 72 pp.

ROBERTSON, K. R. 1975. The Oxalidaceae in the southeastern United States. J. Arnold Arboretum 56: 223–239.

DESCRIPTION OF THE IMMATURE STAGES AND BIOLOGY OF *SYNCLITA TINEALIS* MUNROE (LEPIDOPTERA: PYRALIDAE: NYMPHULINAE)[1,2]

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ABSTRACT. The first and last stage larvae and the pupa of *Synclita tinealis* Munroe are described. In addition, the following biological information was obtained. Duration of copulation was ca. 15 minutes. An average of 82 eggs, which hatched in 5 days at 27°C, was laid. Five larval stages with average head capsule widths of 0.22, 0.28, 0.40, 0.52, and 0.62 mm developed from the eggs and lasted ca. 3.9, 2.8, 3.2, 3.1, and 3.2 days, respectively. The duration of the pupal stage ca. 3 days, and the adult life span ca. 4–5 days. Larvae made silk cases and fed primarily on *Lemna* and *Spirodella*.

The adult male and female of *Synclita tinealis* were described by Munroe in 1972; however, no account was given of the immature stages or biology. The early stages and biologies of two of the three other recognized species in this genus found north of Mexico (*S. obliteralis* (Walker) and *S. occidentalis* Lange) have been studied previously (Hart, 1895; Williams, 1944; Lange, 1956a, 1956b), but in neither case have sufficient details been given of the larval or pupal morphology. The immature stages of the fourth species, *S. atlantica* Munroe, are unknown.

In this paper the first and last stage larvae and the pupa of *S. tinealis* are described and an account is given of its biology and behavior in the laboratory.

MATERIALS AND METHODS

Larvae of *S. tinealis* were collected at four sites in North Carolina: Merchants Mill Pond, Gates Co.; Holt's Pond, Johnston Co.; Pledger's Landing, Tyrell Co.; and Lake Ann, Wake Co. In all cases the host plants were duckweeds (Lemnaceae) of either the genus *Lemna* or *Spirodella*. Several generations were reared from material collected at Merchants Mill Pond; most of the following information is based on this material.

Larvae were reared in either 35 cm³ or 60 cm³ jelly cups or in glass petri dishes. *Lemna*, *Spirodella*, or portions of other host plants were placed in each container, which was then partially filled with water. Moths paired for mating were confined under 300 cm³ plastic cups

inverted over water filled petri dishes containing *Lemna* or *Spiro-della*.

All descriptions and measurements given are of larvae and pupae fixed in KAAD and preserved in ethanol. Genitalia slides were prepared of several reared adult males, and the species was identified by reference to Munroe (1972).

Morphological observations and illustrations were made with the aid of both compound and stereomicroscopes, a camera lucida, and an ETEC Autoscan scanning electron microscope. Material for SEM studies was prepared by critical point drying and gold coating.

The nomenclature of larval setae and punctures follows Hinton (1946), terminology of pupal sclerites follows Mosher (1916), and host plant names follow Radford et al. (1968).

Synclita tinealis Munroe

Synclita tinealis Munroe, 1972: 97.

First Stage Larva

General. Length 1.16–1.38 mm, avg. 1.28 mm. Width at abdominal segment 3, 0.22–0.28 mm, avg. 0.25 mm. Entire larva translucent white. Only 3 ocelli apparently present, corresponding to anterior 3 in last stage larva. Labrum and hypopharynx as in Figs. 3 and 4. Antennae about ½ head capsule length. Mandibles (Fig. 1) pale translucent reddish brown to amber. Cuticle elevated into simple hydrophil papillae covering all body surfaces except head, prothoracic shield, and legs. Diameter of papillae on mesothorax ca. 2.1 μ. Density of papillae ca. 100,000 per mm².

Head. Width 0.19–0.22 mm, avg. 0.22 mm; epicranial index ca. 3.0; antennal segment 2 about 2 times length of segment 1; mandibles ca. 0.05 × 0.06 mm, with 8 to 9 teeth (6 or 7, some showing faint dorsal serrations, along distal margin, and 2 on oral surface near ventral margin); hypopharynx and spinneret as in Fig. 3; labrum as in Fig. 4; setae O1, O2, and O3 in nearly straight line (Fig. 2); O3 closer to SO3 than to O2; distances from A1 to A2 and from A2 to A3 approximately equal; setae A1, A2, A3, and L1 and setae P1, P2, and F1 in approximately straight lines; distance between P2 setae greater than between P1 setae.

Prothorax. Width 0.26–0.28 mm, avg. 0.27 mm; shield and leg sclerites smooth, other areas covered with minute hydrophil papillae; seta D2 4½ times longer than D1, SD1 slightly longer than SD2, L1 4 times as long as L2; SV1 and SV2 subequal in length; distance between XD1 setae greater than between D1 setae; seta XD2 closer to SD1 than to XD1; other setae as in Fig. 5; spiracle apparently absent.

Mesothorax. All surfaces except leg sclerites covered with hydrophil papillae; only one L seta present; other setae as in Fig. 6.

Metathorax. Similar to mesothorax.

Abdomen. Prolegs reduced, crochets on segments 3–6 in narrow, uniordinal lateral penellipse, with posterior hooks slightly larger than anterior hooks; crochets of anal prolegs in transverse uniordinal band; number of crochets on prolegs of segments 3, 4, 5, and 6 and on the anal proleg 17–21, 18–20, 20–22, 18–21, and 8–9 respectively; setae D2, SD1, and L1 relatively long; D2 more than 3 times length of D1, SD2 extremely minute, L1 more than 6 times length of L2; abdominal segments 3–6 with 2 SV setae; only 1 SV seta on abdominal segments 1, 2, 7, 8, and 9; SV2, when present, much shorter and less conspicuous than SV1; on abdominal segment 10 setae D2 and SD2 adjacent with SD2 considerably longer than D2; spiracles apparently absent (Fig. 7).
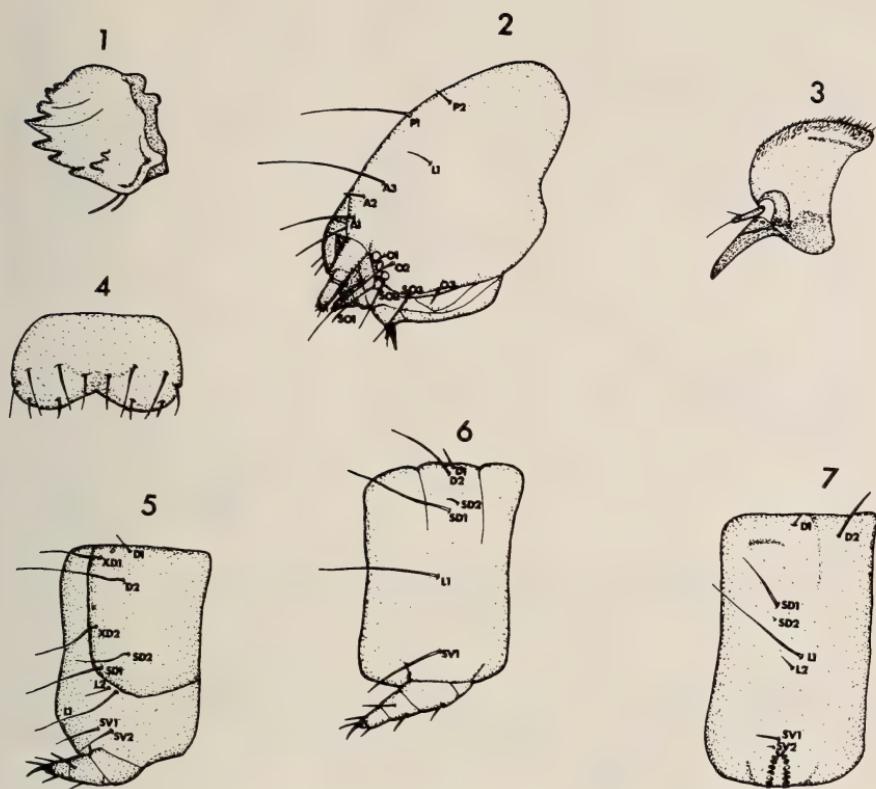
FIGS. 1–7.   1st stage *Synclita tinealis* larva: **1.** right mandible, mesal view; **2.** head, lateral view; **3.** hypopharynx, lateral view; **4.** labrum, dorsal view; **5.** prothorax, lateral view; **6.** mesothorax, lateral view; **7.** abdominal segment 6, lateral view.

Last Stage Larva

General. Length 7.8–9.2 mm, avg. 8.2 mm. Width 1.4–1.6 mm, avg 1.5 mm. Head capsule (Fig. 12) translucent, white to pale brownish-yellow, with darker band extending from behind ocelli to posterior margin; labrum (Fig. 10) pale amber, shallowly notched, with anterior edge dark brown; mandibles (Fig. 9) amber to yellowish-brown, with reddish-brown teeth; hypopharynx and antennae white; spinneret and sclerites of maxillae light brown. Prothoracic shield (Fig. 13) pale amber to light brown, with darker brown spots along top and in arc paralleling ventral and posterior margins; antero-lateral and ventral rim of prothorax unpigmented; remaining areas of thorax and abdomen essentially white. Hydrofuge hairs on all body surfaces except head, anterior ⅓ and entire venter of prothorax, prothoracic shield, anterior ⅔ of venter of mesothorax, thoracic legs, plantae of prolegs, and anal region.

Head. Width 0.59–0.65 mm, avg. 0.62 mm; epicranial index ca. 3.3; surface smooth; antennae long, slender and with antacora elongate and conical; antennal segment 2 about 3 times length of segment 1, both partially retractable into antacora; ocelli 6 in number; nos. 3, 4, and 5 in straight line, with 3 and 4 contiguous; lenses of ocelli 1 and 2 indistinct; ocellus 6 represented by pigmented spot only or apparently absent; mandibles ca. 0.15 × 0.15 mm, with continuous arc of 9 to 11 teeth, including 5 to 6 distal
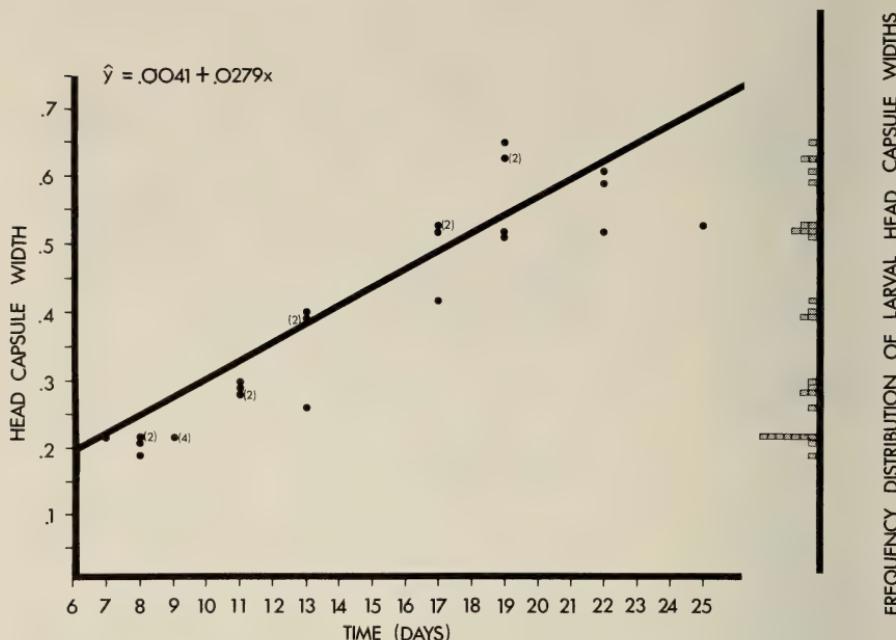
Fig. 8. Linear regression of head capsule width and developmental time of *S. ti-nealis* at 27°C. $R^2 = 0.857$. Eggs laid on day 1, hatched on day 6; pupae present on days 22 and 25; 10 adults emerged on day 25. Frequency distribution of head capsule widths given at right of figure. Each block indicates one larva.

teeth and row of 4 to 5 smaller teeth on oral surface near ventral margin of mandible; two postero-ventral mandibular setae present, both well developed and with anterior seta somewhat longer than posterior seta; hypopharynx and spinneret as in Fig. 11; maxillae with long seta-like processes on mesal surface; labrum and epipharynx as in Fig. 10; setae O1, O2, and O3 in nearly straight line; O3 closer to SO3 than to O2, seta O3 longer than O1, seta O2 much longer than O1 or O3; distance O2 to O3 more than 3 times distance O1 to O2; setae A1, A2, A3, and L1 in nearly straight line; setae A3 somewhat longer than A1; A1 about 2 times length of A2; distances A1 to A2 and A2 to A3 approximately equal; A3 closer to A2 than to L1; L1 and A2 nearly equal in length; setae P1, P2, and F1 in nearly straight line; distance between P2 setae greater than between P1 setae; Af1 and Af2 both very short and thin; F1 of moderate length; C1 usually longer and thicker than C2; S0 setae as in Fig. 12.

Prothorax. Width 0.83–0.92 mm, avg. 0.87 mm; shield and leg sclerites smooth; anterolateral and ventral regions of prothorax with hydrophil papillae; posterolateral region raised and with fine hydrofuge pubescence; spiracle small, ca. 0.03 mm in diameter; D2 about 2½ times length of D1, XD1 and XD2 of approximately equal length, SD2 slightly longer than SD1, L1 much longer than L2, and SV1 slightly longer than SV2; distance between XD1 setae greater than between D1 setae, distance XD1 to XD2 greater than distance XD1 to D1, distance D1 to D2 greater than distance D1 to XD1, distance SD1 to SD2 less than distance SD1 to XD2, and distances XD1 to XD2 and XD2 to SD1 approximately equal; coxae contiguous on midventral line.

Mesothorax. Surface entirely covered with hydrofuge pubescence, except anterior ⅔ of venter, and legs; setae D2, SD1, L1, and SV1 prominent (Fig. 14); D1 and SD2 very small; L2 and L3 minute; separation of coxae ca. 0.03 mm.
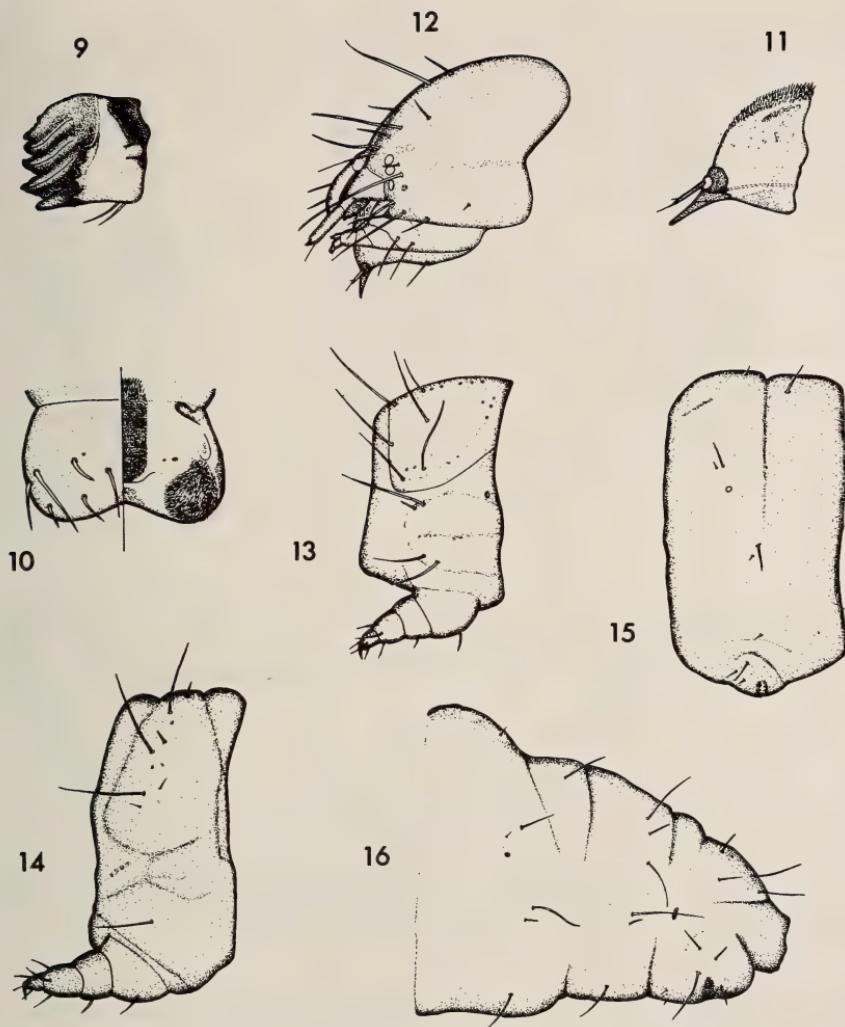
Figs. 9–16. Last stage *Synclita tinealis* larva: **9.** right mandible, mesal view; **10.** labrum (dorsal surface to left and ventral surface to right of vertical line); **11.** hypopharynx, lateral view; **12.** head, lateral view; **13.** prothorax, lateral view; **14.** mesothorax, lateral view; **15.** abdominal segment 6, lateral view; **16.** abdominal segments 8–10, lateral view.

Metathorax. Entire surface, except legs, entirely covered with hydrofuge pubescence; setae as on mesothorax; separation of coxae ca. 0.25 mm.

Abdomen. Prolegs reduced; crochets on segments 3–6 in transverse biordinal bands with anterior hooks larger than posterior, difference becoming more pronounced caudad; crochets of each anal proleg in single transverse biordinal band; number of crochets on prolegs of segments 3, 4, 5, and 6, and on anal proleg 33–39, 34–41, 36–49, 38–44, and 10–12, respectively; all setae on abdominal segments 1–8 greatly reduced in both length and thickness; D2 about 3 times as long as D1, L1 more than 3 times
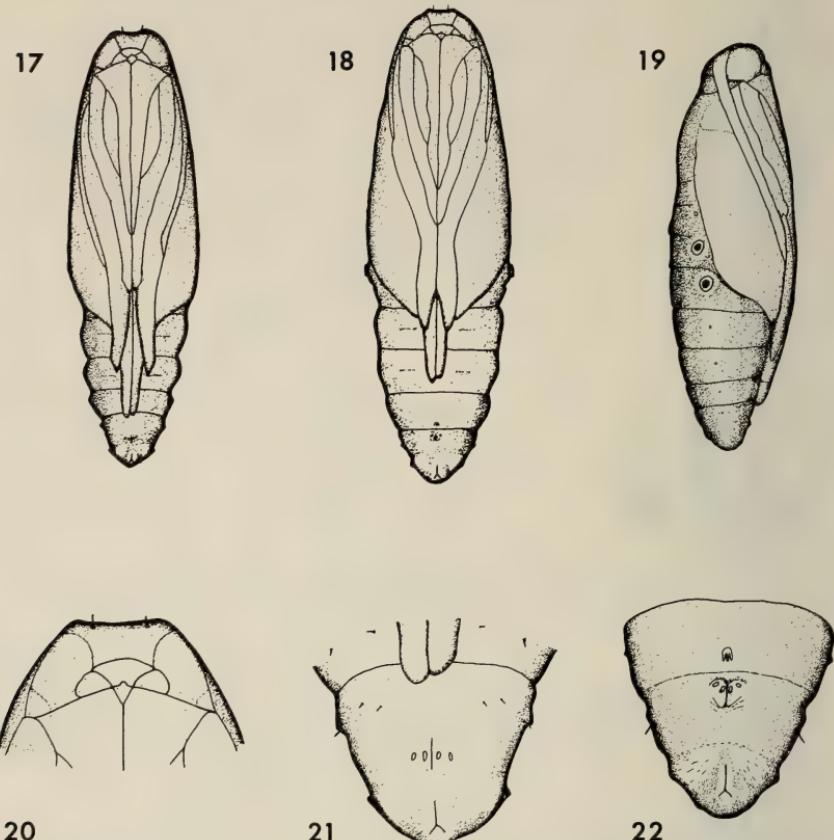
FIGS. 17–22. *Synclita tinealis* pupae: **17.** male pupa, ventral view; **18.** female pupa, ventral view; **19.** male pupa, lateral view; **20.** male pupa, head; **21.** male, abdominal segments 7–10, ventral view; **22.** female, abdominal segments 7–10, ventral view.

length of L2 or L3; distance between D1 setae less than between D2 setae (Fig. 15); 2 SV setae on abdominal segments 1 and 7, 3 present on segments 2–6, only 1 on segments 8 and 9; SV2 and SV3, when present, much shorter and thinner than SV1; on abdominal segment 9 (Fig. 16), setae D2, SD1, and L1 relatively longer than on more anterior segments; SD2 and L3 apparently absent; on abdominal segment 10, D2 and SD2 adjacent and about equal in length; D1 and SD1 less prominent, SD1 equal in length to D1 and located directly ventral of D1; L2 about 2½ times length of L1 or L3 and only slightly closer to L1 than to L3.

Pupa

General. Female (Fig. 18): Length 4.0–5.0 mm, avg. 4.6 mm. Width 1.41–1.51 mm, avg. 1.45 mm. Male (Figs. 17, 19): Length 3.6–3.7 mm, avg. 3.7 mm. Width 1.08–1.09 mm, avg. 1.09 mm. Head, thorax, and abdomen white to pale brownish-yellow, darkening as moth within develops.

Head. Vertex slightly depressed (Fig. 20), epicranial suture absent; labrum distinctly separated from clypeus; pilifers set off as distinct sclerites, separated by labrum and

labial palpi; length of antennae of male ca. 0.5 total body length; length of antennae of female ca. 0.28 total body length; sclerite of labial palpi small, undivided; length of maxillae of male ca. 0.68 length of wings (both measured from caudal margin of labrum); length of maxillae of female ca. 0.55 wing length; maxillary palpi distinct.

Thorax. Prothoracic legs of female extend to segment 3, mesothoracic legs reach middle of segment 5, and metathoracic legs extend just past middle of segment 6; prothoracic, mesothoracic and metathoracic legs of male reach segments 4, middle of 6, and 8 respectively; mesothoracic legs of female broadly joined along midventral line; mesothoracic legs of male separate for entire length; mesothoracic spiracle not visible; tegulae only faintly indicated.

Abdomen. Proleg scars faint but visible on segments 5 and 6; setae very inconspicuous; spiracles of abdominal segment 2 ca. 0.04 mm in diameter; spiracles on abdominal segments 3 and 4 enlarged, somewhat elliptical and situated on raised conical tubercles; dimensions for each spiracle in female ca. 0.18 × 0.16 mm, and in male ca. 0.12 × 0.11 mm; spiracles of segments 5–8 very small, ca. 0.02 mm in diameter, and not readily discernible; segments 6–9 with pairs of small, papilla-like dorso-lateral tubercles, increasing in size on more posterior segments; female genital openings (Fig. 22) confluent, apparently located on segment 8, and flanked by two pairs of papillae; male genital opening (Fig. 21) on ventro-meson of segment 9 and also flanked by two pairs of papillae; unidentified "M"-shaped structure on segment 7 of female, anterior to genital opening.

Material Examined

North Carolina: Gates Co., Merchants Mill Pond, 9 1st stage larvae, 5 last stage larvae, 7 pupae, on *Spirodella polyrrhiza* (L.) Schleiden, *Lemna valdiviana* Philippi, and *Lemna perpusilla* Torrey, 9-II-1975, Coll. P. D. Kinser.

BIOLOGY

The mating behavior of three pairs of moths was observed in the laboratory. Prior to copulation, the female assumed a posture with the abdomen steeply elevated and the ovipositor extruded perpendicularly to the surface on which the moth rested. Males were more active and tended to fly around the enclosure frequently. After the male located and made contact with a female, the female lowered the abdomen and withdrew the ovipositor. In copulation the moths are joined end to end, with the wings of the male resting on those of the female. Mating can occur in either sex within the first day after emergence. Copulation lasted an average of 14½ minutes (10, 17, 16½ minutes), and oviposition started after an average of 48 minutes (28, 84, 32½ minutes). No multiple matings were observed.

In ovipositing, the female moth rested on the host plant and deposited eggs singly or in small groups of up to 10 on the lower surface of the host plant fronds about 1 mm from the margin. The eggs are oval and flattened and measure about 0.52 × 0.40 mm. During development the eggs increase somewhat in size. This has been previously noted by Berg (1950) and Welch (1916) for the eggs of *Munroessa icciusalis* and *Parapoynx maculalis*, respectively. The first oviposition lasted about 24 minutes and an average of 43 eggs was laid. A

second oviposition occurred in two instances about 30 minutes after the first had ceased, and about 20 more eggs were laid. Small numbers of additional eggs were also deposited during the next several days. The total numbers of eggs laid by these and four other moths ranged from 38 to 139 (avg. 82).

The eggs of *Synclita tinealis* were found to hatch in about 1 week (5 days at 27°C, 8 days at 21°C, 13 days at 16°C). The hatching process was not observed, but the newly hatched larvae began feeding and case making during the first day after hatching. No egg or larval cannibalism was observed; the larvae tended to avoid eggs and each other. First stage larvae remained on the under surface of the leaves of the host plant. They began case construction by cutting a groove at the edge of a frond along a semicircular line with a radius about equal to their own length. Then the larva pulled itself, together with the semicircular fragment which it had detached, under the remaining portion of the frond. Next, the larva attached this fragment with silk to the frond. At a later time the larva was seen to cut a matching patch from the upper frond and free the case. These first cases were flat, loosely bound together and had little inner lining. The larva expanded its case gradually by adding additional pieces of frond, or later whole fronds, to the original case. As the larva and its case increased in size, the older portions of the case were often cut off and discarded. The cases of older larvae were increasingly well made. The frond fragments or fronds that were added to the case were bent to conform to the general shape of the larva and firmly attached to the case, which at this time had a delicate silk lining. Several observations were made in which larvae seemed to inspect and lay down a meshwork of silk on all surfaces of a piece of leaf to be added to the case. This possibly facilitated manipulation and provided the prolegs a better grasp of the substrate. Both ends of the case remained open and larvae were observed to turn around in it readily. Feeding and casemaking appeared to be largely uninhibited by light, and larvae fed on any of the surfaces or along the edges of a frond. In some instances in which there was a shortage of the preferred host plant, detritus of various sorts was incorporated into the larval cases. Larvae separated from food withdrew partially from their cases and moved the front halves of their bodies in broad circles in the water until food was located.

Pupation took place in the last larval case, which was completely and densely lined with silk and usually left floating.

Information on the number of larval stages and development was secured from a laboratory culture (Fig. 8). A total of 121 eggs was laid by one moth on March 17 on *Spirodella polyrrhiza* in the laboratory. These were placed in a constant temperature room at 27°C on March

19 and hatched on March 22. The following day 100 larvae were put into separate 35 cm³ jelly cups filled partially with water, into which fronds of *Spirodella* and *Lemna* had been placed. At intervals during the following weeks samples from five cups were taken and the larvae preserved. A total of 45 cups were sampled and 30 larvae recovered. Larvae in the remaining cups had either died or pupated. Head capsule widths were measured and the stages identified as follows: 1st stage: 0.19–0.22 mm, avg. 0.22 mm; 2nd stage: 0.26–0.30 mm, avg. 0.28 mm; 3rd stage: 0.39–0.42 mm, avg. 0.40 mm; 4th stage: 0.51–0.53 mm, avg. 0.52 mm; 5th stage: 0.59–0.65 mm, avg. 0.62 mm. Sampling was discontinued on April 10, as by that time all larvae had pupated and the emergence of adults had begun. Some information was also gained on the developmental times of the larvae and other stages, although a considerable overlap became apparent toward the end of the rearing period. This may have been due to differences in the quality and amount of food given to each larva. At one time many larvae temporarily ran out of food, and in a number of instances, early stage larvae became separated from the host plant and had to be pushed back into contact with it. Sexual dimorphism may also have been a factor. The following approximate durations for each stage were derived from the data that were collected: egg: 5 days; 1st instar: 3.9 days; 2nd instar: 2.8 days; 3rd instar: 3.2 days; 4th instar: 3.1 days, 5th instar: 3.2 days; pupa ca. 3 days; adult: 4–5 days.

Additional observations were made on feeding preference, antagonistic behavior, movement, and defecation. A variety of aquatic plants in diverse families was presented to larvae. These included *Azolla caroliniana* Willdenow (Azollaceae), *Spirodella polyrrhiza*, *Lemna perpusilla*, and *Lemna valdiviana* Philippi (Lemnaceae), *Elodea canadensis* Michaux (Hydrocharitaceae), *Myriophyllum brasiliense* Cambessedes (Haloragaceae), *Potamogeton pulcher* Tuckerman (Potamogetonaceae), *Polygonum* sp. prob. *hydropiperoides* Michaux (Polygonaceae), and *Nuphar luteum* (L.) Sibthorp & Smith (Nymphaeaceae). It was found that plants in the Lemnaceae were preferred, *Azolla*, *Elodea*, and *Myriophyllum* were fed on moderately, and the others, *Potamogeton*, *Polygonum*, and *Nuphar*, were not utilized to any appreciable extent. Larvae under crowded conditions or deprived of food devoured their own cases and those of neighboring larvae; however, the inner layer of frond tissue and the silk lining were usually left. Larvae whose cases were attacked vigorously thrashed from side to side in their cases or more rarely attempted to bite the other larva. In many instances the thrashing alone was enough to prompt the attacking larva to reverse direction in its case and search for food in another direction. This same movement also

was used at times by the larva to effect movement away from adverse situations or to regain contact with the host plant. Defecation in this species was quite forceful, with fecal pellets being propelled some distance from the case.

LITERATURE CITED

BERG, C. O. 1950. Biology of certain aquatic caterpillars (Pyralididae: *Nymphula* spp.) which feed on *Potamogeton*. Trans. Am. Microsc. Soc. 69: 254–266.

HART, C. A. 1895. On the entomology of the Illinois River and adjacent waters. Bull. Ill. State Lab. Nat. Hist. 4: 164–183.

HINTON, H. E. 1946. On the homology and nomenclature of the setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. Trans. R. Entomol. Soc. Lond. 97: 1–37.

LANGE, W. H. 1956a. Aquatic Lepidoptera, pp. 271–288. *In* R. L. Usinger (ed.) Aquatic Insects of California, University of California Press, Berkeley. 508 pp.

———— 1956b. A generic revision of the aquatic moths of North America: (Lepidoptera: Pyralidae, Nymphulinae). Wasmann J. Biol. 14: 59–144.

MOSHER, E. 1916. A classification of Lepidoptera based on the characters of the pupae. Bull. Illinois State Lab. Nat. Hist. 12: 14–159.

MUNROE, E., *in* Dominick, R. B. et al. 1972. The Moths of America North of Mexico, Fasc. 13. 1A, Pyraloidea (in part). The Curwen Press, London, England. 134 pp.

RADFORD, A. E., H. E. AHLES & C. R. BELL. 1968. Manual of the Vascular Flora of the Carolinas. Univ. of N.C. Press, Chapel Hill. 1183 pp.

WELCH, P. S. 1916. Contributions to the biology of certain aquatic Lepidoptera. Ann. Entomol. Soc. Am. 9: 159–187.

WILLIAMS, F. X. 1944. Biological studies in Hawaiian water-loving insects. Part IV. Lepidoptera or moths and butterflies. Proc. Hawaiian Entomol. Soc. 12: 180–185.

A DESERT SUBSPECIES OF *GLOVERIA MEDUSA* (LASIOCAMPIDAE)

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ABSTRACT. A brood of a taxon of *Gloveria* was reared from ova of a wild female taken at Pinyon Flat, Santa Rosa Mountains, Riverside County, California, 11 July 1978. The large, lightly marked ova; the large, darkly colored, hairy larvae; and the food plant of *Quercus turbinella californica* set the taxon apart from *Gloveria medusa* Stkr. The adults are larger, the wings differently proportioned, the markings distinctly different and the color darker in the females than in either *Gloveria medusa* or *Gloveria gargamelle* Stkr. This distinct desert subspecies, *Gloveria medusa editha*, is described.

Gloveria medusa Strecker, 1898, was described from Los Angeles but occurs widely in the coast ranges of southern and central California (Franclemont, 1973), as far north as Monterey. Larvae from this region have been reared by me and by others, and the life history is well known. However, a population of *medusa* that occupies the high desert east of the coast ranges differs from the nominate form in size, color, genital structure, foodplant, and time of emergence. It clearly represents at least a distinct subspecies that I now describe. The type series of 11 males and 15 females was reared from eggs of a female collected with ultraviolet light at Pinyon Flat, elevation 1250 m, Santa Rosa Mountains in the southern Great Basin, Riverside County, California, by John and Ruth Johnson.

Gloveria medusa editha Johnson, **new subspecies**

Ova. Larger than in ssp. *medusa*, one ovum measuring 2.5 mm in diameter and 3.0 mm in height. A ssp. *medusa* ovum from a wild-caught female measured 2.2 mm in diameter and 2.6 mm in height. Ova of ssp. *editha* more pointed at the apex, those of ssp. *medusa* more rounded; apical brown spot of *editha* smaller, white ring surrounding it narrower than these features on *medusa* ova; enveloping brown ring outside white ring less continuous and less dense in *editha* than in *medusa*; two lateral spots of *editha* ova set in smaller white fields, remaining brown pigmentation of chorion less intense and more irregularly distributed than in *medusa* ova (compare Fig. 1: A, B & C).

Larvae. At hatching ssp. *editha* larvae more robust with darker sides and longer setae than those of ssp. *medusa*. The stripe of interrupted addorsal red dashes of the first four instars more vividly red and less orange than in ssp. *medusa*; in later instars, sixth for males and seventh for females, *editha* larvae more densely haired and noticeably darker on sides than larvae of *medusa*; lateral areas of white and grey, so conspicuous on sides of *medusa* larvae, much reduced on *editha* larvae. Refer to Fig. 2, where seventh instar, fully-fed larva of *editha* allotype female, one day before spinning, is photographed with newly moulted, seventh instar, wild-caught, female larva of *medusa*, which has not yet fed to repletion.

Foodplant. Subspecies *editha* larvae fed on *Quercus turbinella californica* Tucker (Munz and Keck, 1959). The newly hatched larvae were transported to their native habitat and offered foliage of *Eriogonum fasciculatum polifolium* (Benth.) S. Stokes and that of other native shrubs and trees, but accepted only turbinella oak. As picked supplies
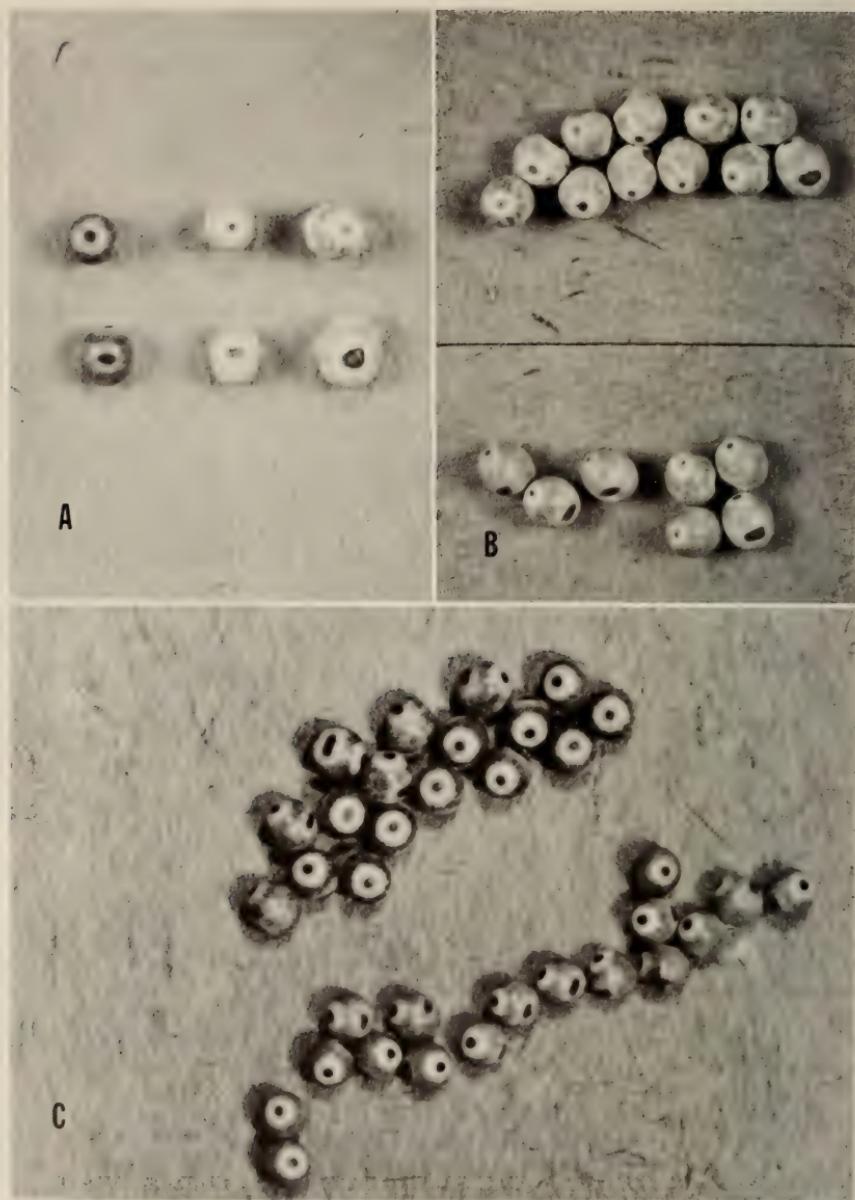
FIG. 1. **A.** From left to right, recently laid ova of *Gloveria medusa medusa*, *Gloveria arizonensis*, and *Gloveria medusa editha*, showing comparative sizes (Bottom row, lateral view; Top row, dorsal view). ×3. **B.** *Gloveria medusa editha* ova. ×2.5. **C.** *Gloveria medusa medusa* ova, somewhat over-enlarged, ×2.7, compared to B.

FIG. 2. **Upper larva:** Fully fed seventh instar larva of the allotype female of *Gloveria medusa editha* on 16 June 1979, one day before spinning. **Lower larva:** Newly-moulted, seventh instar female of *G. m. medusa,* not yet fed to repletion, collected 5 June 1979, Orange Co., California. ×1.

were exhausted, the author offered the more readily available foliage of *Quercus dumosa* Greene, which the larvae accepted. While ssp. *medusa* has been reported from a number of foodplants (Franclemont, 1973), its usual foodplant is one of several varieties of *Eriogonum fasciculatum* Benth. The ssp. *medusa* larva shown in Fig. 2 was found on *Quercus dumosa,* on which it fed poorly, producing a stunted ssp. *medusa* female. This is the only record of the nominate subspecies feeding on oak. As the larvae of *Gloveria medusa* have a tendency to wander about freely at night, the larva may have strayed from nearby *Eriogonum fasciculatum fasciculatum* bushes into the *Quercus dumosa* thicket, where it was found. As with ssp. *medusa,* the larvae of ssp. *editha* fed only at night.

Flight period. Subspecies *medusa* flies in late August and early September, the males being active from about 10:00 A.M. to 4:00 P.M. PDT. Subspecies *editha* flies at Pinyon Flat in July. One field observation suggests that its daily flight time might also be different from *medusa*'s. One, or possibly two, males were seen flying at dusk in the type locality at about 7:30 P.M. PDT, 29 July 1978.

Holotype male. Antennae, head, eyes, thorax, and superior surfaces of primaries dark brown, contrasting strongly with lighter color of secondaries and abdomen. Across primaries, a well-defined, transverse, median band. Discal spot white. Semi-hyaline area in middle of primaries distad of discal spot; submarginal area dark brown, with row of subdued, darker brown spots from apical to inner angle; white setae scattered over primaries, heavier in basal area, along costal margin distad of median band, and

in submarginal area of wings. Primaries of holotype of ssp. *editha* noticeably more pointed and longer in proportion to width than for ssp. *medusa*, the over-all size of the former markedly greater. Holotype forewing length 32 mm, outer margin width 19 mm; compared to mean forewing length of three wild-caught ssp. *medusa* males 29.5 mm, and margin width 18.8 mm. Abdomen and secondaries rich cinnamon brown as for ssp. *medusa*, but caudal tuft of long setae darker on *editha*.

Inferior surfaces: pro- and mesothoracic legs dark brown, metathoracic legs cinnamon brown. Primaries paler than on superior surface; discal spot white; large semi-hyaline patch across median area of wings; basal area cinnamon brown. The *editha* holotype larva spun its cocoon between 8 and 13 June 1979, the adult (Fig. 3) emerging 21 July 1979.

Allotype female. Antennae and eyes black, head black with scattered yellow setae. Thorax covered by shaggy black setae mixed with pale grey setae, latter more numerous on metathorax. Abdomen nearly black with predominantly black setae and with scattered brown and light grey setae. Superior surfaces of the primaries dark grey, nearly black, overlaid by white setae; discal spot white, allotype's transverse median band very faint, band present in some paratypes; submarginal row of black spots absent on allotype, present on some paratypes, but much subdued from apical to inner angle. Primaries proportionately wider than in ssp. *medusa*. Superior surfaces of secondaries dark grey to nearly black, submarginal areas darkest, lacking brown tones of ssp. *medusa*. Secondaries more rounded and ample than in ssp. *medusa*. Inferior surfaces of primaries nearly black throughout, with semi-hyaline area across postmedian field on some paratypes. Inferior surfaces of secondaries nearly black throughout, with white setae and scales along costal and outer margins.

The female allotype larva spun its cocoon on 17 June 1979, the adult emerging 25 July 1979. Length of forewing of allotype female 44 mm; that of wild parent about 46 mm (Fig. 4).

DISCUSSION

Genitalia preparations of two males were made of each ssp., *editha* and *medusa* (Fig. 5). In *Gloveria* the aedoeagus is dorsal between two wing-like alary processes, the endophallus everting from the base of the aedoeagus into a membranous structure. The valves are ventral, enclosing the saccus. Variations were observed in the shape of the aedoeagus of ssp. *medusa*: One was very long and pointed; the second was shorter and blunt at the end. In both *editha* specimens the aedoeagus was heavier and sharply pointed, with a prominent dorsal tooth near the tip and small teeth on the ventral edge. Aedoeagal tooth size and arrangement varied in the pairs of genitalia of both subspecies. In both, the teeth were confined to the distal half of the aedoeagus, unlike the arrangement described for *Gloveria garga- melle* Stkr. (1884) by Franclemont (1973, p. 69; fig. 19).

In *editha* the outer sclerotized portions of the valves ended sharply and abruptly, being more round in *medusa*. The alary processes to either side of the aedoeagus tended to be shorter and wider in *editha* than in *medusa*.

A very consistent and marked difference in the shape of the saccus differentiated the two sets of genitalia. In *editha* the saccus is large and extended, while in *medusa* the saccus is much shorter and smaller.

Fig. 3. **A.** Holotype male of *Gloveria medusa editha*. ×1. **B.** A wild-caught, newly-emerged male of *Gloveria medusa medusa*, collected 18 August 1979, Orange Co., California. ×1.
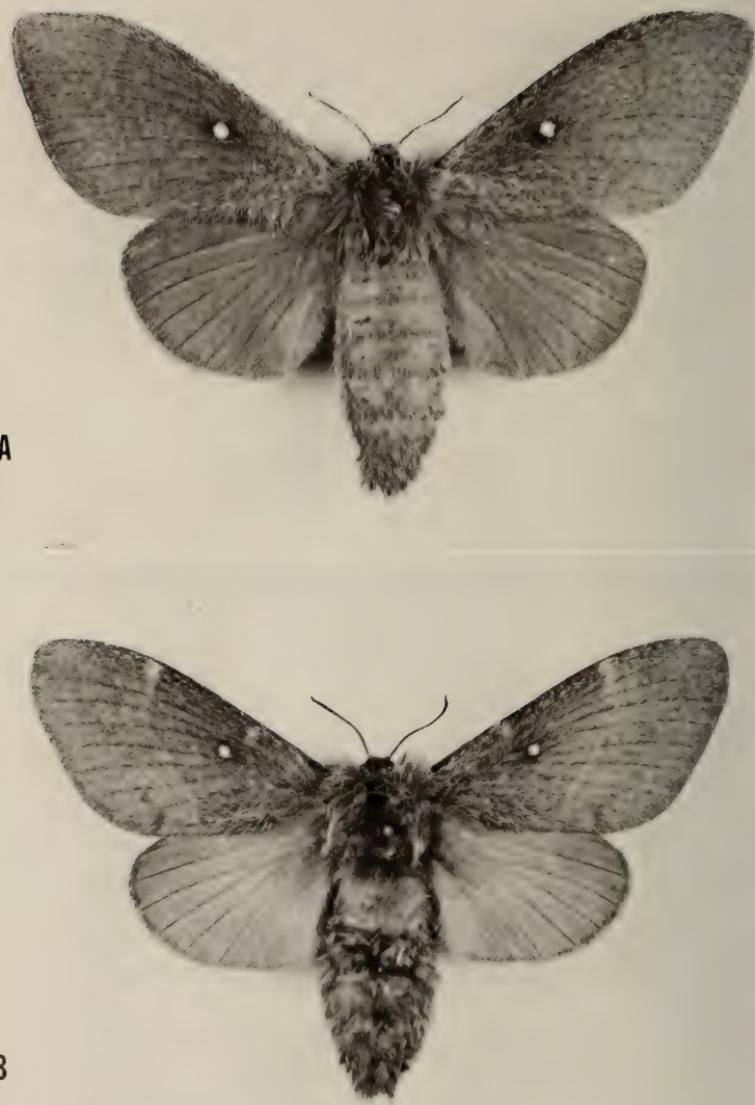
FIG. 4. **A.** Allotype female of *Gloveria medusa editha*. ×1. **B.** Female of *Gloveria medusa medusa*, reared from an ovum taken from wild female, Orange Co., California (contrasting black or brown tones of subspecies not evident in photographs). ×1.
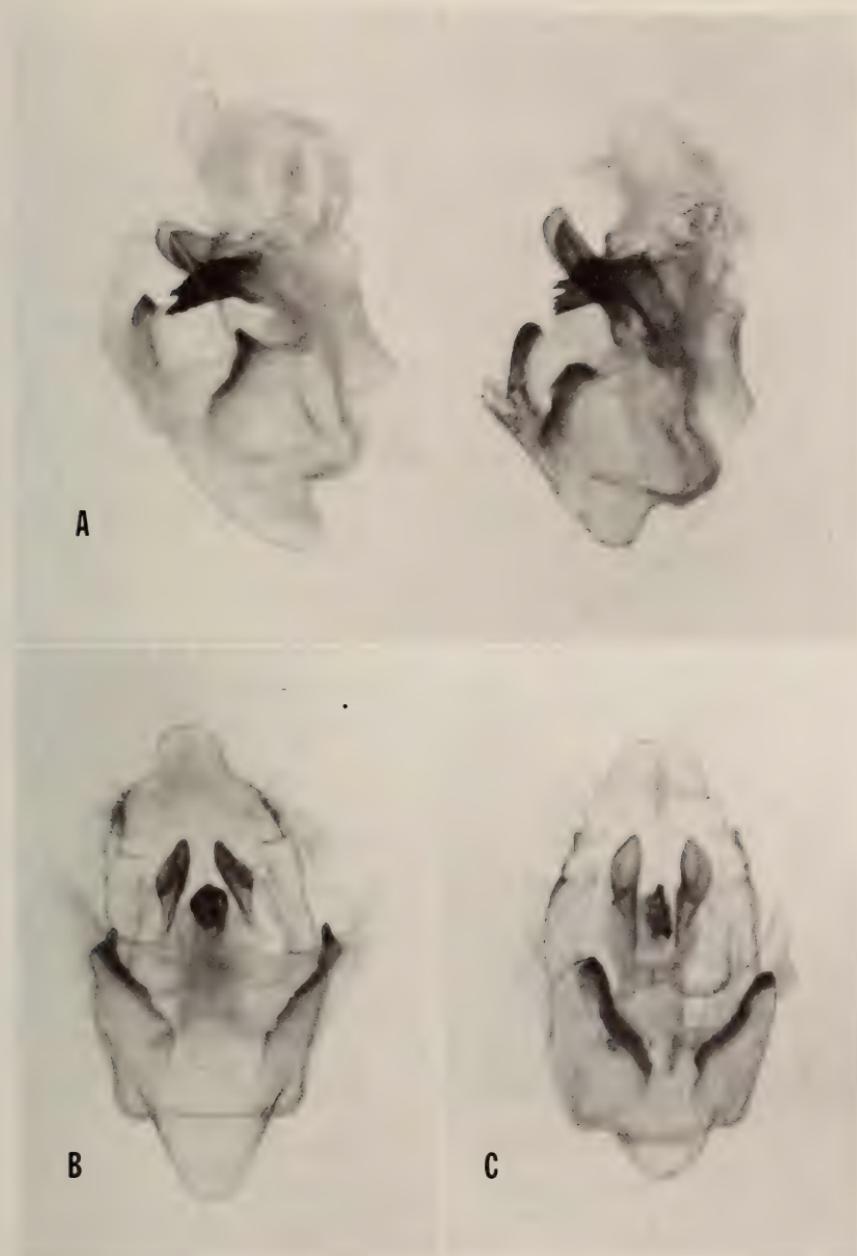
FIG. 5. Male genitalia of the two subspecies of *Gloveria medusa*. **A.** Lateral view: left, *editha*; right *medusa*. **B.** Ventral view: *editha*. **C.** Ventral view: *medusa*. ×25.

Subspecies *editha*, thus, shows many points of distinction from ssp. *medusa* such as: a marked difference in the shape of the genitalia; a marked difference in size and details of wing shape and color in the adults; a difference in the season of flight; distinct differences in the ova, larvae, foodplant, and habitat. Therefore, I believe the subspecific status of the *editha* population is clearly valid and justified.

Some difficulty was encountered in rearing the *editha* larvae. In the native habitat the cold nights of late fall, winter, and spring retard feeding and development until April, when the turbinella oak puts forth new shoots. The larvae then feed and grow rapidly to pupation in June and emergence in July. In the mild coastal climate of Corona del Mar the larvae fed rapidly, reaching the final instar in December and full size in January, one larva spinning on 16 January 1979, the pupa subsequently dying. Most larvae rested through the spring months, feeding only occasionally, gradually shrinking in size due to dehydration and use of internal tissue reserves. Cocoon formation occurred haphazardly. A few larvae resumed feeding in April and May, and from these less stunted specimens, the holotype and allotype were chosen. The holotype and allotype will be deposited in the type collection of the Los Angeles County Museum of Natural History, with a pair of paratypes going to the National Museum, Washington, D.C. Three pairs of paratypes have been placed in Erich Walter's collection, and six male paratypes and ten female paratypes remain in the author's collection.

LITERATURE CITED

FRANCLEMONT, J. G., *in* Dominick, R. B. et al. 1973. The Moths of America North of Mexico. Fasc. 20.1, Mimallonoidea; Bombycoidea (in part): 3–86, pls. 1–11.

MUNZ, P. & D. P. KECK. 1959. A California Flora. Univ. Calif. Press, 1681 pp., 134 figs.

STRECKER, H. 1884. Description of new species of North American Heterocera. Proc. Acad. Nat. Sci. Philadelphia 36: 283–286.

—— 1898. *Lasiocampa medusa* n. sp. Ent. News 9: 13.

GENERAL NOTES

THE OCCURRENCE OF *POANES YEHL* (SKINNER) (HESPERIIDAE) IN KENTUCKY

The first known Kentucky specimens of the Yehl skipper, *Poanes yehl* (Skinner), were taken 15 and 16 September 1979, during a field meeting of the Society of Kentucky Lepidopterists. Males and females in condition varying from fresh to slightly worn were collected by Richard A. Henderson, Leroy C. Koehn, John S. Nordin, and the author in two localities in Fulton County, the westernmost of Kentucky counties.

Both sites were within 5 miles of the Tennessee border. The first captures were in and around swampy woods where State Rd. 94 crosses Little Bayou de Chien, 2.5 miles east of Cayce. The butterflies were visiting blossoms of climbing hempweed, *Mikania scandens* (L.) and goldenrod, *Solidago* sp., or resting on foliage near the ground.

The second site was along a dirt road south from State Rd. 1282 in the Reelfoot National Wildlife Refuge. Swampy woodland bordered the dirt road on one side and soybean fields the other. Several *P. yehl* were taken by the author on blossoms of ironweed, *Vernonia* sp., and at rest on vegetation near the ground. The latest taken in the day was after 5:00 P.M., almost at sunset.

Other species of particular interest collected at these localities were *Euphyes dion dion* (Edwards) and *Lethe portlandia missarkae* Heitzman & dos Passos (both sites), and *Lethe appalachia* R. L. Chermock (common at the first site). These records are the first for these species in September in Kentucky. Collections of these and others of the 46 species recorded during the trip were made by William R. Black, Jr., and James R. Merritt, in addition to those named above.

On 21 June 1980, *P. yehl* was observed in both localities mentioned above by Henderson, Nordin, and Loran Gibson in company with *E. dion* and *Poanes viator* Edwards. The Yehl skipper was seen on flowers of button bush, *Cephalanthus occidentalis* L., American germander, *Teucrium canadense* L., and red clover, *Trifolium pratense* L.

Finally, the author took 1 female Yehl skipper on mistflower, *Eupatorium coelestinum* L., in Graves County, Kentucky, at a field-woods interface on the Bell farm near Kaler. This record extends the known range about 30 miles northeastward from the Cayce site. That site was also visited on 13 and 14 September 1981, and *P. yehl* were moderately common. Many were seen on late thoroughwort, *Eupatorium serotinum* Michx., as well as flowers listed above for 1979.

These records for *P. yehl* may extend the known range slightly northward in its western extremity. Howe (1975, Butterflies of North America, Doubleday & Co., Inc., Garden City, New York, p. 456) reports it from Tennessee, and J. R. Heitzman (pers. comm.) says it is "very local in extreme southern Missouri." This addition brings the Kentucky state butterfly list to 132 recorded species.

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RESPONSES BY BUTTERFLIES TO SEASONAL CONDITIONS IN LOWLAND GUANACASTE PROVINCE, COSTA RICA

The recent report on *Agrias* in Costa Rica (DeVries, 1978, J. Lepid. Soc. 32: 310) warrants further comment with regard to the locality of capture for *A. amydon* Hew. *Agrias amydon* was captured in the Santa Rosa National Park in the lowlands of the

Guanacaste Province, a region characterized by a strong annual dry season. DeVries did not mention the date of capture, although the dry season in this region generally occurs between December and June, and lasts 6–7 months. However Daniel H. Janzen originally captured this species at the beginning of the dry season in Santa Rosa and subsequent captures have been made later in the dry season here as well as at other localities across the Cordillera Central into the Atlantic lowlands (by P. DeVries). This note will attempt to explain the occurrence of *A. amydon* and other typically wet forest Nymphalidae in highly seasonal lowland tropical regions (such as Guanacaste) throughout the year, and will suggest the existence of two different ecological mechanisms promoting butterfly activity in both wet and dry seasons.

The lowland Guanacaste dry season is a period of considerable environmental stress to both plants and insects, save for riparian forest habitats that remain fairly evergreen (Janzen, 1967, Evolution 21: 620–637; 1976, Brenesia 8: 29–34). The riparian evergreen forest environment in Guanacaste near the end of the dry season is noticeably cooler, both for air and soil temperatures; has higher relative humidity than nearby deciduous forest habitats (Janzen, 1976, op. cit.); and provides a more favorable microclimate for organisms requiring moist conditions for their activity. *Agrias* and the majority of other forest nymphalid butterflies of Neotropical regions attain their highest diversity (defined here as the number of species in a region) in both lowland and montane tropical wet forests (Seitz, 1924, Macrolepidoptera of the World, Vol. 5, The American Rhopalocera, A. Kernan, Stuttgart; A. M. Young, pers. obs. 1968–1979, in Costa Rica).

On the eastern slopes of the Cordillera Central in Costa Rica, and in the eastern lowlands, the annual dry season is relatively short and slight, and adult nymphalids are generally active throughout the year at the same localities along an altitudinal "transect" from about 1000 m to 90 m above sea level at one latitude (A. M. Young, pers. obs.). Nymphalid genera such as *Historis, Adelpha, Prepona, Siproeta, Anaea* and many others are active throughout the year along such a transect. Undoubtedly, adults in small, highly fragmented forest populations of *Agrias* are also active throughout the year along the eastern slopes of both the Cordillera Central and Talamanca ranges.

A major feature of the more seasonal lowland Guanacaste region is an explosion of "leafing out" and other forms of vegetative growth in both herbaceous and woody plants at the beginning of the wet season (Janzen, 1967, op. cit.). Such conditions provide a greatly expanded food base for herbivores such as larval Lepidoptera. During the severe dry season, small adult populations of typically wet or moist forest butterflies, such as the blue form of *Morpho peleides,* at least two species of *Anaea,* several Papilionidae (including *Parides* and *Battus*) and other butterflies, occur in pockets of evergreen riparian forests, which are like present day refugia. But as the wet season begins and advances these populations increase in size. Furthermore, "corridors" of leafed-out vegetation occur between the lowland and higher elevational forest areas along the western slopes of the Cordillera Central during the wet season, promoting expansions of montane butterfly populations into suitable lowland areas in Guanacaste. During the dry season some butterflies undoubtedly migrate into nearby mountain forests to escape from desiccation in deciduous forest habitats in the lowlands. Paul A. Opler (Office of Endangered Species, Dept. of Interior) has studied seasonal distributions of butterflies in Guanacaste. In the particular case of the pierid *Eurema daira* he has discovered that a "wet season phenotype" of predominantly females migrates into the mountains early in the dry season, to be replaced later in the dry season by a "dry season phenotype" which stays in the lowlands. Both phenotypes are present in riparian forests in the lowlands, the aggregations of the adults shifting continually in response to changes in adult food supplies (Opler, in prep.).

Seasonal changes in vegetation and habitats at this time may be less pronounced at higher elevations on the western slopes, thus providing supplemental refugia for many butterflies in addition to lowland evergreen riparian forests. As a result, nymphalids and other butterflies in the northwestern region of Costa Rica have available two different less stressful (in terms of moisture and food resources) environments: lowland evergreen riparian forests and pockets of moist forest higher up on the slopes of the Cordillera Central.

Under the conditions discussed above, the butterfly fauna of the region is in a dynamic state of changing habitat associations and changing localities, both at a given altitude and along an altitudinal gradient (20–1200 m). The captures of *A. amydon* during the Guanacaste dry season by Janzen and DeVries in both forest and open pasture habitats indicates that adults of this species probably pass most, or all, of the long dry season primarily associated with forest refugia. During the dry season, strong-flying *A. amydon* and perhaps other nymphalids undoubtedly forage in open areas, only to return to sheltered retreats in response to thermal stress. Furthermore, the spectrum of forest habitats present at Santa Rosa undoubtedly provides different types of refugia for butterflies during the dry season, perhaps more so than for other localities in Guanacaste. It is expected that not all butterfly species will respond to dry season stress in the same manner; thus, while some species such as *A. amydon* may pass this period associated primarily with forest refugia but with occasional foraging in open pastures near shaded buildings (such as for the site of Janzen's original capture), others may migrate to higher elevations as observed by Opler. In addition to responding to thermal stress and availability of adult food supplies, the degree to which a butterfly species passes the dry season in the Guanacaste lowlands will also be dependent upon the condition of larval host plants and whether or not adults experience reproductive diapause. Species with very deciduous larval host plants will either remain in the lowlands in reproductive diapause or migrate into higher elevations where host plants might still be verdant. Further field studies of many different nymphalids can be conducted to examine these alternative suggestions more critically.

The lesson to be learned from observing butterflies in the tropical dry season, in terms of the ecological features of seasonal tropical environments affecting the survival ability of relatively small poikilotherms, is the need to distinguish between resident and migrant species at particular localities at different times of the year. If done, it may not be unusual to find moist or wet forest butterfly species in highly seasonally variable regions of the American tropics. What appears to be emerging from the fragmentary data gathered to date is that butterfly species occupying lowland tropical regions with specific seasonal changes, such as that exemplified by lowland Guanacaste Province in Costa Rica, may exhibit different strategies for passing the dry season. The strategy of a given species may be of one kind in that adults either occupy riparian forest patches acting as ecological refugia or migrate to less seasonal higher elevation habitats where both adult and larval resources are available. The first strategy also promotes the evolution of reproductive diapause. Or, as indicated by the interesting work of Opler, some species may exhibit a "mixed" strategy in which complex polymorphisms generate different morphs, each a specialist for a different strategy. In some ways the expressed phenotypic polymorphism of a species such as *Eurema daira* (Opler, in prep.) is a generalist strategy, permitting adaptation to the existing dry season conditions of the lowlands, while providing an escape-valve from the resource-depleting effects of the season.

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OBSERVATION OF AN AGGREGATION OF *EPISCADA HYMENAEA* PRITTEV. (ITHOMIIDAE) IN PARAGUAY

A large aggregation of *Episcada hymenaea* Prittev. was observed at 1630 hr, 50 minutes before sunset on 21 July 1979. The location of the aggregation was a wooded area 90 m above sea level bordering an unnamed stream 0.5 km NNW of the intersection of the railroad with Avenida Mcal. Lopez (the principal SW to NE road) in Areguá, Departamento Central, Paraguay. The habitat was a dense forest of shrubby trees 5 to 7 m in height. The temperature was 20°C, the sky was clear, and there was no wind. Thousands of the butterflies rested closely together on the foliage of at least two species of trees over an area approximately 75 × 25 m in extent. Each individual stood in a plane parallel to the surface on which it rested. Within this plane the long axis of the body was as nearly vertical as possible with the anterior above the posterior end. The butterflies could be quietly approached, but flew off when a branch was shaken or when attempts were made to catch them by hand.

Evidence was observed which may reflect on the cause of the aggregation. First of all, the presence of the butterflies on various species of plants suggests that oviposition was not involved. Second, the absence of any pupal exuviae precludes the possibility of a mass emergence. The facts that July is in the middle of the season of abundance of this day-flying species in the Areguá area and that the observation took place at a time of rapidly waning light suggest that the aggregation was the result of the sum of local movements at the end of a period of activity.

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A LOCALIZED ABERRATION IN *SATYRIUM CALANUS FALACER* (LYCAENIDAE) IN NEW JERSEY

On the afternoon of 24 June 1980, while collecting near Lakehurst, New Jersey (Ocean County), I captured six aberrant *Satyrium calanus falacer* (Godart) on which the postmedian band of the ventral forewing was connected to the cell-end bar by horizontal bands. In addition I found several specimens displaying intermediate characteristics. Four of these butterflies are illustrated in Fig. 1.

What is so unique about this catch is that within a two hour period all of these were caught while feeding on the same patch of dogbane (*Apocynum*). Over the next two weeks I especially sought and failed to find additional aberrant specimens during my collecting in Bergen and Sussex Counties, New Jersey and Rockland County, New York. I returned to Lakehurst on 5 July and collected 247 *falacer* from various collecting sites near this town. Of these, three were similar to the above; two were col-

FIG. 1.   Aberrant specimens of *Satyrium calanus falacer*, ventral surface.

lected at this initial site, while the other was caught within 100 yards of this spot. Eight of the specimens are female and one is a male.

I wish to express my thanks to Dr. Clifford D. Ferris for helpful comments in the preparation of this manuscript.

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FRASS-BOUND FIRST INSTAR LARVAE OF *CITHERONIA REGALIS* (SATURNIIDAE)

During the course of rearing hundreds of larvae of *Citheronia regalis* (Fabricius), I lost occasional ones soon after their hatching, until I discovered what was amiss. Many of the eggs had been detached from where a female had glued them. A larva, chewing itself out of such an egg, sometimes failed to emerge all the way. Ordinarily a larva is able to crawl completely out of its anchored shell. These larvae succeeded in extending themselves until they had straightened out, but their anal prolegs remained within the eggshell. When they now undertook to walk, the true legs and anterior prolegs functioned normally, but the rear prolegs simply carried the shell along.

Consequently, after the larvae began to feed, their frass was ejected into the eggshell. Within several days the shell became filled to such an extent that it could hold no more. Meanwhile, the accumulating fecal material had exerted increasing pressure on the larval body, constricting it at the shell's opening. Thus, fecal impaction resulted

from two causes, and larvae ultimately died from inability to pass food through their bodies.

I eventually found that it was easy to pull away adhering eggshells from day-old larvae with fine-tipped entomological forceps. Lepidopterists rearing rare species from limited supplies of eggs should be alert to this readily avoided loss.

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JÄCKH COLLECTION OF MICROLEPIDOPTERA TO THE SMITHSONIAN INSTITUTION

With substantial assistance from the United States Department of Agriculture, the Smithsonian Institution has recently acquired a major collection of European Microlepidoptera. Begun in 1923, the Eberhard Jäckh collection now totals more than 53,000 superbly prepared specimens. The collection is especially strong for the middle European fauna with more than 90% of the known species represented. Mr. Jäckh also collected extensively in northern Italy, Yugoslavia, as well as the United States, and has exchanged specimens widely with colleagues from other European countries. Some of the major groups of Lepidoptera particularly well represented in the collection are the Pyraloidea (9000 specimens), Tortricoidea (12,000 specimens), Gelechioidea (10,000 specimens) and Tineoidea (6000 specimens).

The quality standards of the Jäckh's collection are unsurpassed. Mr. Jäckh's meticulous technique of spreading live specimens, anesthetized by ether, undoubtedly produces the finest results. All specimens are not only expertly spread but are also fully labelled and identified. The scientific value of the collection is further enhanced by the presence of more than 7500 genitalic preparations. Approximately 30 holotypes and several hundred paratypes are included, and these numbers are steadily growing as Mr. Jäckh continues his studies.

Closely associated with the main collection are extensive reference card files and a well-documented library, including an annotated catalogue of the European Microlepidoptera. The latter is supplemented by copious photographs of adults and genitalic dissections. Also included in the library is a synoptic leaf mine herbarium representing the hosts from many of Mr. Jäckh's rearings.

Eberhard Jäckh was born in 1902 and was early influenced by E. Martin Herring, who first instructed him in Microlepidoptera. Although professionally employed as an aeronautical engineer until his retirement in 1967, Mr. Jäckh, since 1923, devoted as much time as possible to his "second profession," entomology. From 1946 until 1967 he was honorary curator of entomology at the Übersee Museum in Bremen, West Germany. During his varied career, he has published more than 50 entomological papers. Mr. Jäckh now resides with his wife Inge in the small village of Hörmanshofen in Bavaria. Supported by a duplicate portion of the collection temporarily retained by him, Mr. Jäckh continues to enlarge and improve the collection as well as to complete several research papers.

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NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of the collection and study of Lepidoptera. Contributors should prepare manuscripts according to the following instructions.

Abstract: A brief abstract should precede the text of all articles.

Text: Manuscripts should be submitted in *triplicate*, and must be typewritten, *entirely double-spaced*, employing wide margins, on one side only of white, 8½ × 11 inch paper. Titles should be explicit and descriptive of the article's content, including the family name of the subject, but must be kept as short as possible. The first mention of a plant or animal in the text should include the *full scientific name*, with *authors* of zoological names. Insect measurements should be given in *metric units*; times should be given in terms of the *24-hour clock* (e.g. 0930, not 9:30 AM). Underline only where *italics* are intended. References to footnotes should be numbered consecutively, and the footnotes typed on a separate sheet.

Literature Cited: References in the text of articles should be given as, Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and all must be listed alphabetically under the heading LITERATURE CITED, in the following format:

SHEPPARD, P. M. 1959. Natural selection and heredity. 2nd. ed. Hutchinson, London. 209 pp.
——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10: 165–216.

In the case of general notes, references should be given in the text as, Sheppard (1961, Adv. Genet. 10: 165–216) or (Sheppard 1961, Sym. R. Entomol. Soc. London 1: 23–30).

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CONTENTS

JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

The object of the Lepidopterists' Society, which was formed in May, 1947 and formally constituted in December, 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

Membership in the Society is open to all persons interested in the study of Lepidoptera. All members receive the *Journal* and the *News of the Lepidopterists' Society*. Institutions may subscribe to the *Journal* but may not become members. Prospective members should send to the Treasurer full dues for the current year, together with their full name, address, and special lepidopterological interests. In alternate years a list of members of the Society is issued, with addresses and special interests. There are four numbers in each volume of the *Journal*, scheduled for February, May, August and November, and six numbers of the *News* each year.

Cover Illustration: Adult male *Anthocharis sara* Lucas (Pieridae) on inflorescence of fiddleneck (*Amsinckia intermedia* Fischer & Meyer, Boraginaceae). These butterflies occur in central Arizona during spring, often flying through small canyons and washes. Their larvae feed on a wide variety of mustards (Cruciferae). Original drawing by Dr. Rosser W. Garrison, Calle Iris UU18B, Rio Piedras, Puerto Rico 00926.

FACTORS INFLUENCING THE ABUNDANCE AND DISTRIBUTION OF TWO AQUATIC MOTHS OF THE GENUS *PARARGYRACTIS* (PYRALIDAE)

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ABSTRACT. Two species of aquatic pyralid moths of the genus *Parargyractis* occur sympatrically in parts of northern California. The larvae of both species have similar resource requirements, but have different tolerances to parameters of water quality. Thus, the areas of sympatry reflect locations where tolerances overlap. In such areas, larvae interact with the more aggressive species acquiring suitable shelters for larval web construction and pupation sites. Interactions of this type are density dependent, and related to population levels and the number of suitable shelters on submerged rocks. Principle factors influencing larval populations include water velocity, water temperature, and dissolved oxygen concentrations. *Parargyractis jaliscalis* was more tolerant to lower dissolved oxygen concentrations, reduced water velocity, and higher water temperatures than *P. confusalis*, due to different physiological and behavioral adaptions. Physical parameters of water quality strongly influence the distribution and abundance of both species.

The pyralid genus *Parargyractis* consists of aquatic moths. The eggs, larvae, and pupae of *Parargyractis* live underwater in streams, rivers, and occasionally in lakes. On emergence from the cocoon, the adult floats or swims to the surface of the water and climbs onto debris or protruding rocks, where the wings expand. Moths mate on land, after which the female re-enters the water to oviposit on submerged rocks. The first instar larvae respire cutaneously, while those in the second through fifth instars have gills (Fig. 1). The larvae feed on algae and diatoms under or near silken tents, which are constructed over cracks or crevices on submerged rocks. They pupate in a specially constructed cocoon, which has openings near the periphery to allow circulation of water around an inner cocoon, which contains the
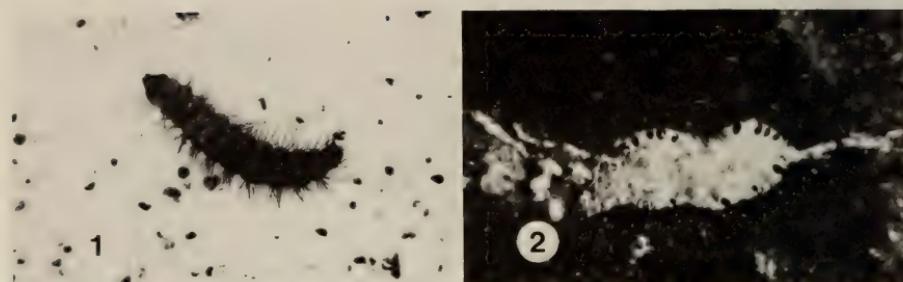
FIGS. 1–2.   *Parargyractis confusalis* **1,** mature larva (3.2×); **2,** cocoon (2×).

pupa (Fig. 2) (Lange, 1956; Tuskes, 1977). Aquatic moths may be common near suitable larval habitat and are a familiar group to aquatic biologists. Munroe (1972) listed 14 species in this genus, which occur north of Mexico.

Two species, *P. jaliscalis* (Schaus) and *P. confusalis* (Walker), were found to occur sympatrically and provided an opportunity to study the mechanisms which allow closely related species to coexist. Both species are widely distributed and are among the few members of the genus that are common as far north as Canada. In California each species has two to three generations per year, and their biology makes them particularly well suited for this type of study. The shelters which larvae construct provide them with territories, which restrict their movements, allowing manipulation of larvae with minimal disturbance, since rocks may be transported in water to the laboratory or other field locations.

METHODS

Physical parameters which might influence the distribution of either species were examined. These included concentrations of nitrate, phosphate, carbon dioxide, dissolved oxygen, and pH, as well as water temperature and velocity. Water velocity was measured with a counter-type pigmy flow meter, which was calibrated at the U.C. Davis Hydraulics Laboratory. All physical parameters were measured at each site approximately 18 times a year.

Field studies were conducted in northern California. Allopatric populations of *P. confusalis* were studied at: Middle Fork of the American River, 8 km S.E. of Auburn, Placer Co., elev. 160 m; and the North Fork of Cache Creek, 11 km N. of Bartlett Springs, Lake Co., elev. 380 m. An allopatric population of *P. jaliscalis* was studied in Putah Creek, 2.6 km S.W. of Davis, Yolo Co., elev. 17 m. Sympatric populations were studied at: Bear Creek, 3.7 km N. of Hwy 20, Colusa

Co., elev. 365 m; and Little Stony Creek, 4.2 km W. of Lodoga, Colusa Co., elev. 365 m.

Behavioral observations in the field were frequently difficult to interpret; therefore, laboratory populations of both species were established. Larvae were collected and placed in 40 to 110 liter aquariums with algae covered rocks. Water was circulated with a bubbling air stone under a plexiglas stand, which directed the rising bubbles at an angle oblique to the surface. Debris on top of the plexiglas stand provided a suitable area on which adults could perch following emergence. A divider, which extended from the bottom to 3 cm above the surface of the water, was used to separate the columns of water moving in opposite directions and improve circulation. A constant current was necessary, because the cocoon is oriented so that water circulates through it.

To examine factors limiting distribution *confusalis* larvae attached to rocks were collected, and the number of larvae per rock was determined. The rocks with larvae were then transported in containers of water to another location in the same stream occupied by only *jaliscalis*. Rocks with larvae of *jaliscalis* attached were treated in a similar manner and transported to a typical *confusalis* habitat. The larvae of each species were left in the habitat of the other species from 1600 to 0900 h. During this time oxygen and carbon dioxide concentrations were monitored at hourly intervals. At the end of approximately 17 h the larvae were removed and transported in well oxygenated water to the laboratory, where mortality was determined. Larvae showing no sign of activity after two hours were considered dead.

Laboratory studies were conducted to determine the effects of oxygen stress. Larvae of both species were collected and maintained separately under similar conditions for 24 h before the tests to determine if any larvae had been injured. One liter flasks were filled with water collected from a stream inhabited by both species. The desired O_2 level was attained by bubbling N_2 through the water. The O_2 concentration was monitored with an IBC differential oxygen analyzer. For each test, five larvae of each species were placed in a 1 liter flask at 22°C and the top sealed with a double layer of Parafilm. After 8 h the seals were removed and the oxygen concentration measured again. The larvae were then placed in Petri dishes containing well oxygenated water (11 ppm). At 10 min intervals, immobile larvae were touched with a probe and considered dead if no movement was noted during a period of 2 h.

Overwintering habits were studied at Bear Creek from late October

to April. Rocks, which were naturally fused in a conglomerate to the stream bed, were selected for similar texture, orientation to current, and larval distribution. During each sampling period larvae were removed from $1/6$ of the surface area of each rock, and returned to the laboratory, where they were sorted to species and instar. The density on each rock was determined, and the average density of each species was calculated. The total area sampled varied ±44.5 cm²; therefore, samples were standardized by multiplying density by the typical sample size of 1090 cm².

RESULTS

Changes in the larval densities of both species were correlated with water temperature and velocity. During the winter months at water temperatures of 1.7 to 11°C, larvae were active but slow to develop. The peak in *confusalis* larval populations occurred during late spring when water temperatures were above 12°C but below 25°C. An aquatic fungus, which is parasitic, was associated with this species when the water temperature rose above 21°C. The density of *jaliscalis* increased when water temperatures were above 17°C and continued to do so throughout the summer. Larvae of *jaliscalis* appeared resistant to fungal attack at all temperatures observed in the field.

Though some larvae occurred in still water, densities of both species were highest in flowing water. Peak densities of *jaliscalis* larvae occurred in velocities ranging from 0.2 to 1.1 m/sec, with a maximum of 1.7 m/sec. Larvae of *confusalis* were most abundant in velocities from 0.3 to 1.4 m/sec, with some occurring in velocities as high as 2.6 m/sec.

Fig. 3 shows a typical O_2-CO_2 profile for two different habitats in the same creek but separated by 5.1 km. Diurnal O_2 concentrations were sufficiently high to support both species, but at night O_2 concentrations were too low for *confusalis* in areas of abundant algal growth, due to dark phase respiration. In habitat A there was from 120 to 190 times more algae (dry weight) than in habitat B. During the summer oxygen concentrations in habitat A frequently declined to 2 ppm at night. The lowest O_2 concentration recorded for habitat B was 6.8 ppm. Habitat A represented a normally allopatric population of *jaliscalis*, while B was an area occupied by *confusalis*. Only 2.0% of the 181 *jaliscalis* larvae transported to the *confusalis* habitat died (this may have been handling injury), while *confusalis* larvae moved to the *jaliscalis* habitat incurred 34.5% and 27.7% mortality (n = 96, 108). Levels of NO_3 and PO_4 were very low and did not appear to be influencing either species.

The overwintering study indicated that during a 6 month period
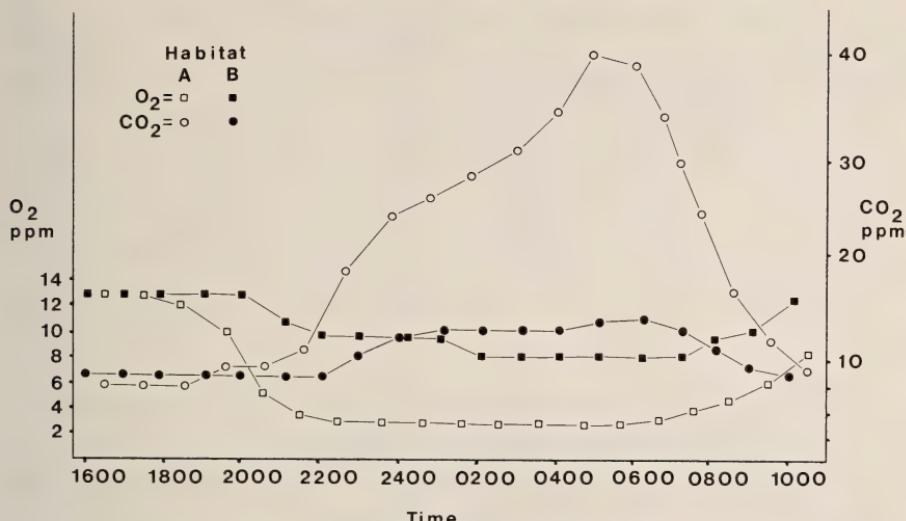
FIG. 3.   Aquatic oxygen, carbon dioxide profile of Bear Creek, Lake Co., Calif. Habitat A represents an area inhabited by only *P. jaliscalis*. Habitat B is an area dominated by *P. confusalis*.

(October to April) the larval density of *confusalis* decreased by 25.5%. During this same period, the decrease in the *jaliscalis* population was 71% (Table 1). No samples could be taken during February, due to high water.

In the laboratory *jaliscalis* larvae were more aggressive than those of *confusalis* and moved across the rock surface, frequently attempting to enter the webs of *confusalis*. In approximately 16% of such encounters, the larvae of *confusalis* were displaced. Second or third instar larvae of *jaliscalis* were found within the cocoons of *confusalis*, and it was observed that many of these pupa usually failed to hatch. Occasionally the pupa was found to be damaged by the intruding

TABLE 1. Changes in larval density during overwintering, Bear Creek.

| | P. confusalis | | | | | | | P. jaliscalis | | | | | |
| | No. collected & instar | | | | | | Den. | No. collected & instar | | | | | Den. |
Date	2	3	4	5	Total	% Δ	/cm²	2	3	4	5	Total	% Δ	/cm²
October 30	8	42	38	29	117	—	.113	3	23	20	48	94	—	.090
December 31	0	12	41	48	101	−18.0	.093	0	0	22	50	72	−25.5	.067
January 31	0	0	24	72	96	−5.5	.088	0	0	2	31	33	−54.5	.030
March 30	0	0	0	98	98	+1.0	.087	0	0	0	26	26	−21.0	.024
April 30	0	0	0	92	92	−3.5	.084	0	0	0	21	21	−20.5	.019

% Δ = % change in density from previous month.
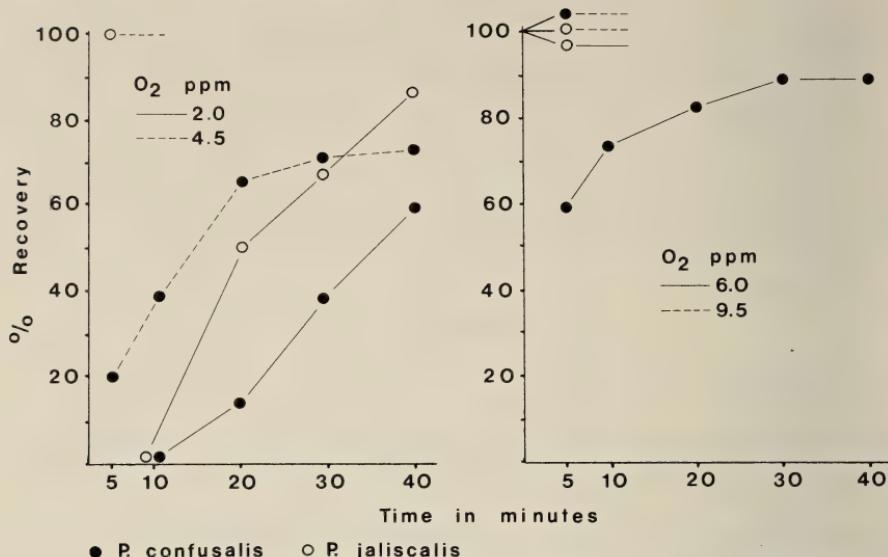
FIG. 4.   Recovery and mortality rates of *P. jaliscalis* and *confusalis* last instar larvae which were subjected to varying degrees of oxygen stress.

larva, but the usual cause of pupal death was believed to be suffocation resulting from the larva disrupting the circulation of water around the pupa. No *jaliscalis* larvae were observed entering a conspecific's web. Unlike *jaliscalis* larvae, those of *confusalis* were not observed to displace or attempt to enter another individual's web.

The number of gills per larva in the second through fifth instar of both species differs significantly (P < 0.05) (Table 2). The gills of both species are about the same size, but the larvae of *jaliscalis* had from 24 to 43% more gills than *confusalis* of the same instar. Larvae of *jaliscalis* exhibited a greater tolerance to lower O_2 concentrations than *confusalis*, as they recovered faster with lower mortality than *confusalis* under similar oxygen stressed conditions (Fig. 4).

DISCUSSION

Field and laboratory observations indicate that both *P. confusalis* and *P. jaliscalis* can, and do, exist sympatrically. *Parargyractis jaliscalis* is the predominant species in the Central Valley of California, while *confusalis* is more abundant above the valley floor in both the Coast Range and the Sierra Nevada. A number of factors influence the distribution of *confusalis*.

Behavioral observations suggest the larvae of *jaliscalis* are more active and aggressive and may enter the cocoons of *confusalis* through

TABLE 2. Comparison of gill number per larval instar between *P. jaliscalis* and *P. confusalis*.

| Instar | *P. jaliscalis* | | *P. confusalis* | | |
	Average # of gills	S.D.	Average # of gills	S.D.	t
2	47.35	3.65	39.70	2.85	14.82
3	136.70	7.38	76.70	3.56	19.38
4	174.14	5.10	123.24	6.62	18.41
5	208.00	6.18	160.84	7.10	13.82

S.D. = Standard Deviation.
Sample size equals 40 individuals per instar/species.

openings around the cocoon's periphery (Fig. 2). This intrusion usually resulted in the death of the pupa. Such interactions are density dependent phenomena, and occur primarily when the number of suitable locations for web or cocoon construction is low in relation to larval density.

In areas which undergo nocturnal oxygen stress, morphological and physiological adaptations to this stress influence the distribution of larvae. In each larval stage that utilizes gills, *jaliscalis* has from 24 to 42% more gills than *confusalis* (Table 2), and thus, has a correspondingly greater gill surface area for respiration. In addition to differential mortality at O_2 concentrations below 5 ppm (Fig. 4), the larvae of *jaliscalis* remained active longer and recovered faster than *confusalis* under identical O_2 stress. In areas of sympatry *confusalis* was infrequently observed where the dissolved oxygen concentration is below 7.2 ppm. However, in allopatric areas *confusalis* was found to occur where the oxygen concentration frequently reached a minimum of 5.25 ppm. Laboratory experiments also indicated that *confusalis* can exist at O_2 levels 1.5 to 2.0 ppm less than that observed in areas of sympatry. It appears that *jaliscalis* is better adapted to warmer, less well oxygenated water, and this, combined with its aggressive nature, allows it to out-compete *confusalis* when the O_2 concentration is below 7.0 to 7.5 ppm.

Physical factors and a reduced competitive advantage limit the distribution of *jaliscalis*. Although *jaliscalis* larvae are abundant in the fall, samples in sympatric areas indicate a substantial decrease in larval density throughout the winter. It was found that 30 to 60% of the *jaliscalis* larvae are dislodged from rocks following the first substantial rain of the season. The mortality is related to maximum water velocities, with higher mortality occurring in swift portions of the stream, especially where water velocity exceeds 1.2 m/sec. A survey of larval distribution along a water velocity gradient during the sum-

mer indicated that *confusalis* larvae occurred in velocities as high as 2.6 m/sec, while the maximum for *jaliscalis* was 1.7 m/sec. As water velocity increases the active behavior of *jaliscalis* larvae becomes a disadvantage; for when they leave the shelter of their silken webs, they are swept away by the current.

Of the two, *jaliscalis* larvae are more active and adapted morphologically and physiologically to slower, warmer, less well oxygenated water. *Parargyractis confusalis*, on the other hand, is better adapted to colder, fast flowing, well oxygenated water. Though each species utilizes similar resources, each has a refuge, or a portion of its niche which is non-overlapping with that of its potential competitor. During the course of the year, the ability of the larvae to withstand various combinations of physical factors influences the abundance and distribution of each species. These factors play an important role in the outcome of density dependent larval competition between these two aquatic moths.

LITERATURE CITED

LANGE, W. H. 1956. Aquatic Lepidoptera. *In* Aquatic Insects of California. Ed. R. L. Usinger. Univ. Cal. Press, Berkeley and Los Angeles, pp. 271–288.
MUNROE, E. 1972. The Moths of America North of Mexico. Fascicle 13.1a (Pyraloidae) (in part). Classey, London, pp. 116–129.
TUSKES, P. M. 1977. Observations on the biology of *Parargyractis confusalis*, an aquatic pyralid (Lepidoptera: Pyralidae). Can. Ent., 109: 695–699.

TWO NEW SPECIES OF THE TRIBE EUCOSMINI (TORTRICIDAE)

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AND

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ABSTRACT. *Phaneta cruentana* and *Eucosma fritillana* are described. Imagines and male and female genitalia are figured.

Phaneta cruentana A. Blanchard and E. Knudson, new species
Figs. 1, 3, 5

Head: Palpi yellowish white, exceeding front by one eye diameter. Frons and vertex yellowish white with darker scaling centrally. Antennae simple, white with dark dorsal and ventral longitudinal stripes.

Thorax: Patigia yellowish white shading to orange at tips. Tegulae yellowish white. Mesonotum yellowish white to orange near center.

Abdomen: Yellowish white.

Maculation (Fig. 1): *Forewing:* Ground yellowish white with light brown fascia. Costal strigulations dark brown. Inner half of wing thickly clothed with orange red scales to outer fifth. Ocelloid patch divided vertically, inner half buff, outer half yellowish white with a few black scales. Terminal row of white tipped black scales. Cilia orange at apex, buff below. *Hindwing:* ashy gray with grayish white cilia.

Venation: *Hindwing:* M3 and Cu1 anastamosing halfway between lower outer angle of cell and outer margin. M2 well separated from stalk of M3 and Cu1. Rs and M1 approximate towards base.

Length of forewing: Males, 6.4–8.0 mm, average 7.3 mm; females, 7.2–7.8 mm, average 7.6 mm.

Male genitalia (Fig. 3): Slide A.B. 4513, paratype from type locality, 28.VI.78.

Female genitalia (Fig. 5): Slide A.B. 4439, paratype from type locality, 6.X.66.

Holotype: Male, Engeling Wildlife Management Area, near Tennessee Colony, Anderson Co., Texas, 28.VI.78, deposited in the National Museum of Natural History (NMNH) (No. 76733); collected by A. & M. E. Blanchard.

Paratypes: Same locality as holotype, 6.X.66, 1 female; 28.VI.78, 11 males, 2 females; all collected by A. & M. E. Blanchard. 12.VI.80, 4 females; collected by E. Knudson. In addition, there is a female specimen in the NMNH with a white label "Dallas, Texas" and a yellow label "Fernald Collection." We labeled it as a paratype although it lacks an abdomen and the wings need careful respreading.

Remarks

Dr. Richard Brown who has examined some of the specimens comments: "*P. cruentana* appears to be closely related to *P. griseocapitana* (Walsingham) and *P. imbridana* (Fernald). The presence of the well defined brownish orange patch on the inner margin of the forewing of *cruentana* distinguishes this species from the latter two. The male genitalia of *cruentana* are more similar to *griseocapitana* than to *imbridana*. The dorsolateral corners of the tegumen are rounded
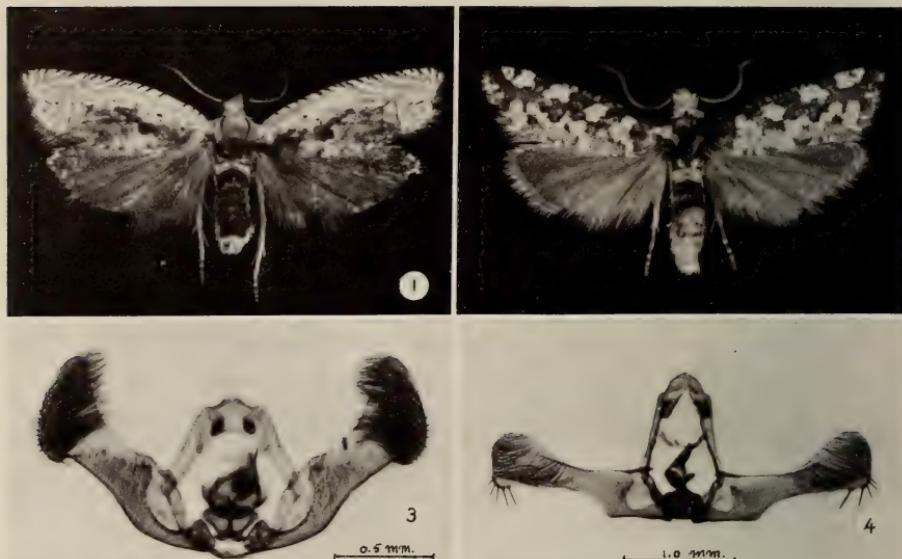
FIGS. 1–4. Holotypes: **1,** *Phaneta cruentana*; **2,** *Eucosma fritillana.* Male genitalia: **3,** *P. cruentana*; **4,** *E. fritillana.*

in *cruentana* and lobed in *griseocapitana*. The ventral emargination of the valva neck is deeper in *griseocapitana* than in *cruentana*. The female genitalia of *griseocapitana* and *imbridana* have not been compared with *cruentana*."

Eucosma fritillana A. Blanchard and E. Knudson, **new species**
Figs. 2, 4, 6

Head: Palpi white dorsally, white speckled with brown ventrally, exceeding front by half an eye diameter. Frons and vertex creamy white. Antennae simple, white.

Thorax: Tegulae and patigia light brown with white tips. Mesonotum light brown.

Abdomen: Light buff.

Legs: Femora white, tibia and tarsus banded with white and gray brown.

Maculation (Fig. 2): *Forewing:* Ground brownish gray (individual scales gray with brown tips giving a powdery appearance). Variable creamy white spots, some of which are partially outlined by dark brown scales. White strigulations over inner half of costa. Cilia white. Hindwing light brownish gray, cilia white.

Venation: *Hindwing:* Cu1 and M3 united. M2 from base of stalk of Cu1 and M3. Rs and M1 approximate towards base.

Length of forewing: Males, 6.8–8.7 mm, average 7.6 mm; females, 7.6–8.9 mm, average 8.1 mm.

Male genitalia (Fig. 4): Slide A.B. 4514, paratype from type locality, 28.VI.78.

Female genitalia (Fig. 6): Slide A.B. 4601, paratype from type locality, 28.VI.78.

Holotype: Male, Engeling Wildlife Management Area, near Tennessee Colony, Anderson Co., Texas, 28.VI.78, deposited in the National Museum of Natural History (No. 76734); collected by A. & M. E. Blanchard.

Paratypes: Same locality as holotype, 28.VI.78, 17 males, 7 females; all collected by
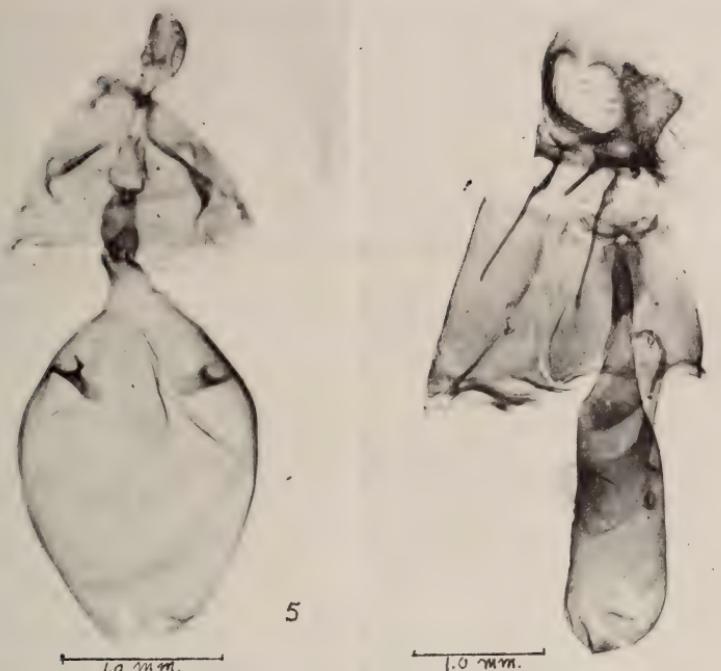
FIGS. 5, 6.   Female genitalia: **5,** *Phaneta cruentana;* **6,** *Eucosma fritillana.*

A. & M. E. Blanchard. 5 miles west of Buffalo, Freestone Co., Texas, 29.IV.78, 3 males; same locality as holotype, 12.VI.80, 11 males, 3 females; all collected by E. Knudson.

REMARKS

Dr. Richard Brown examined some of the specimens and comments: "*E. fritillana* appears to be closely related to *E. robinsonana* (Grote). The two species can be easily separated by forewing color and pattern. The light brown and creamy white markings of *fritillana* are less contrasting than the dark brown and white markings of *robinsonana*; the pattern is banded in *robinsonana* and irregularly checkered in *fritillana*. In the male genitalia, *fritillana* has larger socii, a more angular ventral margin of the sacculus, and fewer and smaller spines on the cucullus than *robinsonana*. The female genitalia of the two species lack distinctive differences."

ACKNOWLEDGMENTS

some of the type material, comparing it to known species, and providing the comments that appear above.

We are also grateful to the Texas Parks and Wildlife Department for their continued interest and cooperation, and to the manager and his associates at the Engeling Wildlife Management Area, near Tennessee Colony, Texas, for their assistance and hospitality during our collecting trips there.

GENERAL NOTE

LONGEVITY ESTIMATES OF FOUR INDIVIDUAL BUTTERFLIES

It has been stated that little is known about how long butterflies live (Howe, 1975, The Butterflies of N. Amer., Doubleday and Co., Inc., N.Y.). As a by-product of tagging and marking for Professor Urquhart's migration studies, longevity estimates of four common California butterflies were obtained. The alar tags with Urquhart's address and a serial number were used in some cases, and in others, alar tags with my phone number were used. Also, colored spots and bars made with a felt tipped marker on the wings were used. All butterflies tagged and marked were wild and of unknown age when caught and released.

Three butterfly species were marked and tagged in a suburban Citrus Heights, California yard and adjacent acre-sized pasture. It was mostly *Plantago lanceolata*, *Trifolium repens*, and a variety of unknown grasses. The yard was mixed unknown grasses. The trees were *Quercus wislizenii*, *Catalpa speciosa*, *Juglans hindsii*, and *Fraxinus velutina*. There were various flowering shrubs.

A *Precis coenia* (Huber) (Nymphalidae) was marked 27 August 1977 and recaptured 14 days later on 10 September 1977 in the pasture. There is hesitancy in reporting such a short period of time, since it migrates, and therefore, it must live for several months. However, after three years tagging and marking 1947 individuals and recapturing 147, 14 days was the longest period obtained for this species. A female *Pieris rapae* (Linnaeus) (Pieridae) was marked 27 May 1977 and recaptured 39 days later on 5 July 1977 in the yard. Two hundred and forty-two were recaptured out of 1494 marked over a ten year period. A *Papilio rutulus* (Lucus) (Papilionidae) was tagged 15 April 1971 and recaptured 39 days later 24 May 1971. Ninety-four were recaptured out of 957 tagged in 11 years.

In a woodland in the Sierra Nevada foothills about three miles southeast of Loomis, Placer County, California, dominated by *Q. wislizenii*, *Baccharis pilularis* and a variety of unknown annual grasses, a *Battus philenor* (Linnaeus) (Papilionidae) was tagged 3 April 1971 and recaptured 44 days later on 13 June 1971. One hundred and thirty-eight were recaptured out of 636 marked and tagged in four months.

The tagged and marked butterflies recaptured and cited here were apparently in good shape; consequently, there is no telling how long they lived. For this reason these results are given as longevity estimates.

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TWO NEW SPECIES OF *EUCOSMA* HÜBNER (TORTRICIDAE) FROM TEXAS

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ABSTRACT. Two new species in the family Tortricidae, *Eucosma griselda* and *Eucosma salaciana*, are described. Imagines and male and female genitalia are figured. Imagines and female genitalia of *Eucosma ridingsana* Robinson are also figured.

Eucosma griselda A. Blanchard & E. Knudson, **new species**

Head: Front ochreous brown. Vertex light ochreous. Labial palpi exceeding front by one eye diameter, ochreous brown with prominent tuft on second segment. Antennae simple, lightly pubescent, ochreous brown.

Thorax: Patagia and tegulae ochreous brown. Mesonotum silvery white with central third ochreous brown. Posterior tuft silvery white.

Abdomen: Light ochreous brown.

Forewing (Figs. 1, 2): Ground color ochreous brown with 6 or 7 well defined silvery patches, each bordered by a single row of dark brown scales. In the female (Fig. 2), the costal silvery patch nearest the base is partially or completely divided near its midportion by an extension of ground color from the costa. In the male (Fig. 1), this costal patch is not interrupted and does not extend as far basad as in the female. The bar-like median basal silvery patch is thicker in the male than in the female. Fringe light ochreous.

Hindwing (Figs. 1, 2): Pale brown. Fringe whitish brown.

Length of forewing: *Males:* (N = 28), 11.1–13.9 mm, average 12.7 mm. *Females:* (N = 15), 10.0–13.7 mm, average 12.6 mm.

Venation: *Forewing:* Termen straight to very slightly concave. Veins R4 and R5 well separate at their bases. Veins M2, M3, and Cu1 nearly parallel, not approximate at termen. *Hindwing:* Veins M3 and Cu1 stalked for ⅔ or much more of their lengths, rarely united to termen.

Male genitalia (Fig. 3): Slide A.B. 594, from paratype, Big Bend Nat. Park, Brewster Co., Texas, 14-V-66.

Female genitalia (Figs. 4–11): Fig. 4 is a view of the entire genitalia and Fig. 5 shows the genitalia following removal of the ovipositor, 8th segment, and tergite of the 7th segment. Figs. 6–11 are enlargements of the ostium bursae region in a series of preparations like that of Fig. 5.

Holotype (Fig. 1): Male, Chisos Basin, Big Bend Nat. Park, Brewster Co., Texas, 7-IV-67, collected by A. & M. E. Blanchard, deposited in the U.S. National Museum of Natural History (NMNH).

Paratypes: Big Bend Nat. Park, Brewster Co., Texas; Chisos Basin, 11-V-66, 2 females, 12-V-66, 1 male, 14-V-66, 1 male, 1 female (Fig. 2), 7-IV-67, 5 males, 9-IV-67, 2 males; Oak Spring, 11-V-66, 2 males, 1 female, 8-V-72, 1 male; Gov't. Spring, 13-V-66, 1 female, 27-III-71, 2 males, 28-III-71, 2 males, 1 female; Green Gulch, 5-IV-67, 1 female, 31-III-71, 2 males, 3-V-72, 1 male, 2-VI-73, 1 female; K-Bar Ranch, 22-III-71, 2 males; Dugout Wells, 30-III-71, 1 male, all collected by A. & M. E. Blanchard. Jeff Davis Co., Texas; Ajuga Canyon, 1-IV-67, 1 male; Ft. Davis, 18-V-71, 1 female, 21-V-71, 2 females, all collected by A. & M. E. Blanchard; Davis Mts. State Park, 29-V-79, 1 female, collected by E. Knudson. Sierra Diablo Wildlife Management Area, Culber-
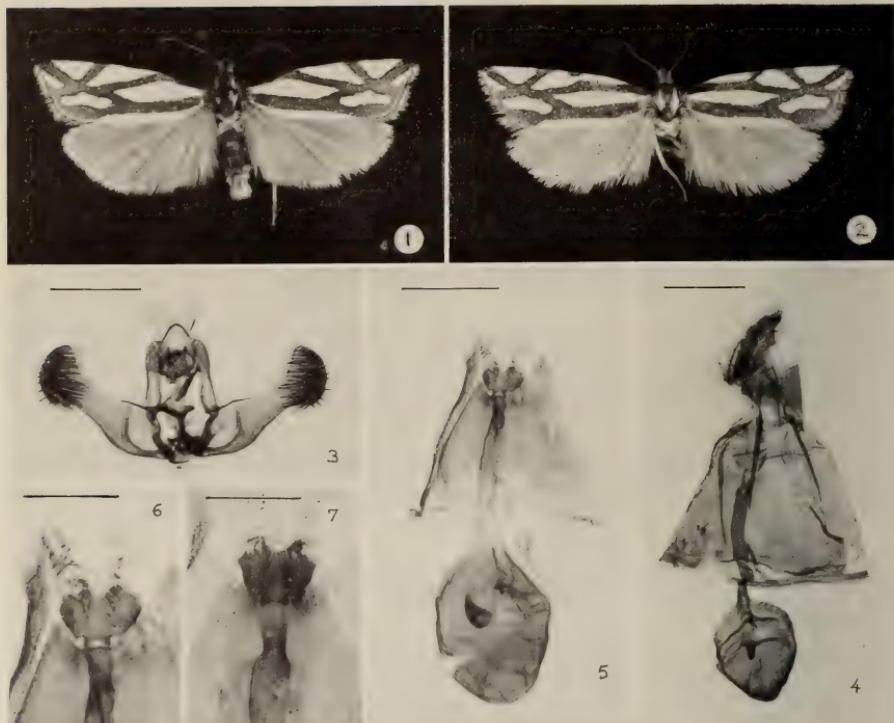
FIGS. 1–7. *Eucosma griselda*; **1,** holotype male, Big Bend Nat. Park, Texas, Chisos Basin, 7-IV-67, A. & M. E. Blanchard coll.; **2,** paratype female, Big Bend Nat. Park, Texas, Chisos Basin, 14-V-66, A. & M. E. Blanchard coll.; **3,** male genitalia, paratype, slide A.B. 594, Big Bend Nat. Park, Texas, Chisos Basin, 14-V-66, A. & M. E. Blanchard coll.; **4,** female genitalia, paratype, slide A.B. 4995, Big Bend Nat. Park, Texas, Gov't. Spring, 13-V-66, A. & M. E. Blanchard coll.; **5,** female genitalia, paratype, slide A.B. 4967 (by E.C.K.), Culberson Co., Texas, Sierra Diablo W.M.A., 30-V-73, A. & M. E. Blanchard coll.; **6,** post-vaginal plate from specimen in Fig. 5; **7,** post-vaginal plate, paratype, slide A.B. 4988, Big Bend Nat. Park, Texas, Oak Spring, 11-V-66, A. & M. E. Blanchard coll. (Line scales in Figs. 3, 5 represent 1 mm; Fig. 6 equals 0.5 mm.)

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FIGS. 8–21. **Figs. 8–11.** *Eucosma griselda*, pre- and post-vaginal plates of female paratypes; **8,** slide USNM 25150 (by A.B.), Cave Creek Canyon, Chiricahua Mts., Arizona, 20-V-66, J. G. Franclemont coll.; **9,** slide A.B. 4990, Big Bend Nat. Park, Texas, Green Gulch, 28-III-71, A. & M. E. Blanchard coll.; **10,** slide A.B. 4992, Sierra Diablo W.M.A., Culberson Co., Texas, 30-V-73, A. & M. E. Blanchard coll.; **11,** slide A.B. 4993, Ft. Davis, Jeff Davis Co., Texas, 21-V-71, A. & M. E. Blanchard coll. **Figs. 12–21.** *Eucosma ridingsana*; **Figs. 12, 13.** adults; **12,** male, Estes Park Colorado, 1-VIII-67, A. & M. E. Blanchard coll.; **13,** female, 6 miles west of Telluride, San Miguel Co., Colorado 15-VII-77, D. C. Ferguson coll.; **Figs. 14–21.** pre- and post-vaginal plates of females: **14,** slide USNM 25146 (by A.B.), Provo, Utah, Tom Spalding coll.; **15,** slide USNM 25147 (by A.B.), Snake River, Whitman Co., Washington, opp. Clarkston, 13-IX-37, J. F. G. Clarke coll.; **16,** slide USNM 25148 (by A.B.), Tenkiller Lk., Cokeson, Oklahoma, 25-VIII-56, D. R. Davis coll.; **17,** same data as Fig. 13, slide USNM 25149 (by A.B.); **18,** slide USNM 25151 (by A.B.), Boulder, Montana; **19,** slide A.B. 4970, Paducah, Cottle Co., Texas, 22-IX-68, A. & M. E. Blanchard coll.; **20,** slide A.B. 4971,
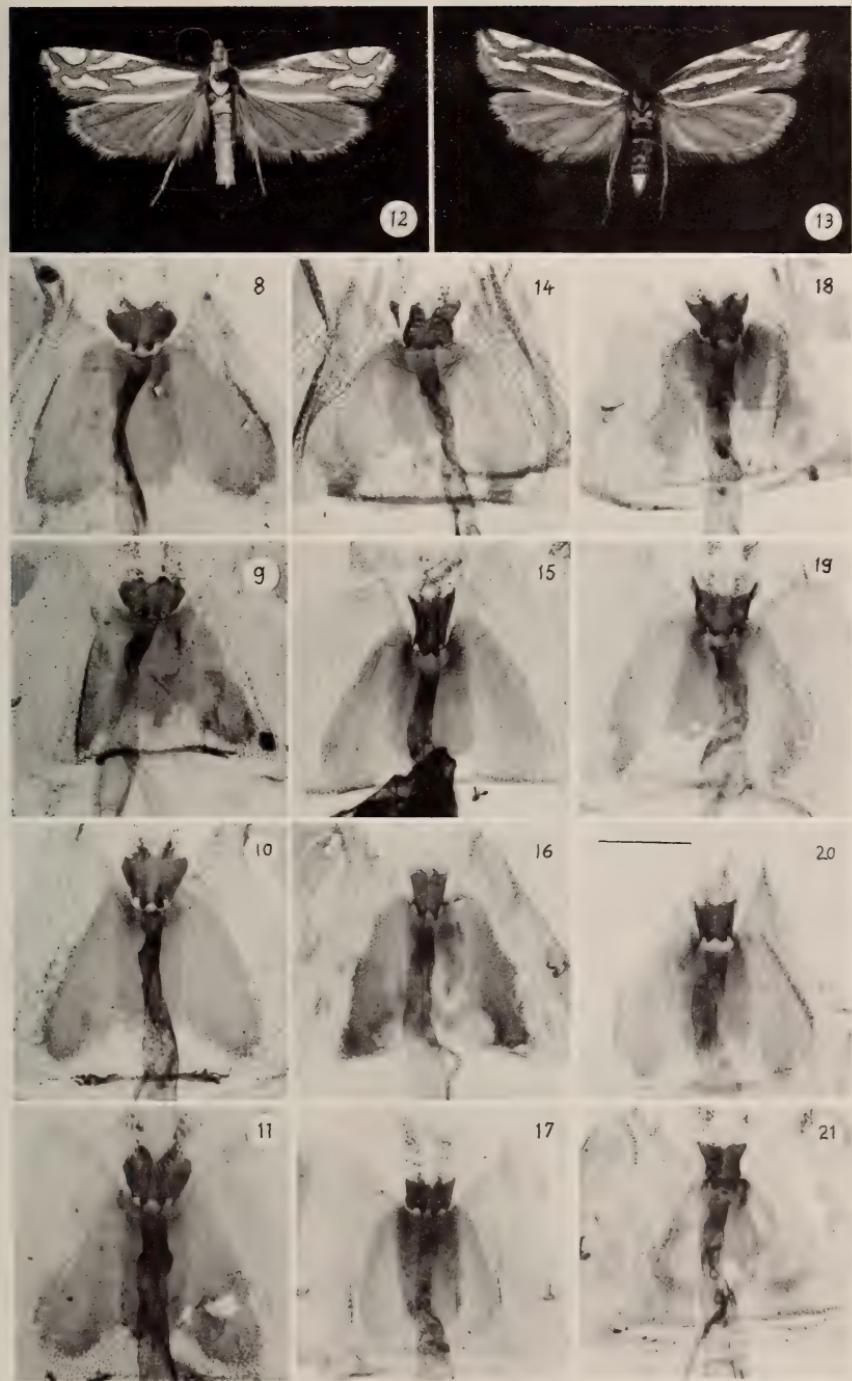
Estes Park, Colorado, 25-VII-68, A. & M. E. Blanchard coll.; **21**, slide A.B. 4989, Guadaloupe Mts., Bear Canyon, Texas, 3-IX-69, A. & M. E. Blanchard coll. (Line scale on Fig. 20 equals 1 mm; all genitalia to same scale.)

son Co., Texas, 27-V-73, 3 males, 29-V-73, 1 male, 30-V-73, 3 females, all collected by A. & M. E. Blanchard. Cave Creek Canyon, Chiricahua Mts., Cochise Co., Arizona, 20-V-66, 1 female, collected by J. G. Franclemont.

REMARKS

This species is extremely similar to *Eucosma ridingsana* Rob., from which it differs in the following points: Size: *E. ridingsana* averages smaller than *griselda*. Maculation: The silvery patches on *griselda* tend to be less irregular and more rounded than those on *ridingsana* and the ground color of *griselda* is darker and more brownish. Female genitalia: Differs in the post-vaginal plate as shown in Figs. 6–11 and 14–21. Distribution: *E. ridingsana* has a wide range throughout the western U.S. and Canada, with records in Texas from far west to central and extreme southern portions. *E. griselda* is known only from far west Texas and southeastern Arizona, although it probably occurs in similar habitats in southern New Mexico and north central Mexico. Flight period: *E. ridingsana* has a fairly long flight period extending from June through November, although most examples from Texas are from September and October. *Griselda* flies from late March to early June.

Since *griselda* is so close to *ridingsana* and undoubtedly has been previously unrecognized in collections, it seemed necessary to illustrate in detail a structural character that can serve to reliably separate the two species. Therefore, the female genitalia were carefully studied, using a method of dissection in which all extraneous structures are removed to allow optimal view of the pre- and post-vaginal plates. Dissections were performed on the majority of females in the authors' series, including examples of *griselda* from Texas, and *ridingsana* from Texas and Colorado. In addition, examples of *ridingsana* were studied from Utah, Montana, Washington, and Oklahoma, and a single female of *griselda* was studied from Arizona. The results are shown in Figs. 6–11 (*griselda*) and Figs. 14–21 (*ridingsana*). In *griselda*, the post-vaginal plate is wider with outer margins convex. In *ridingsana*, the lateral margins are straight or concave, and the caudal apices tend to be produced, in most cases extending well beyond the mid portion of the caudal margin. Although there is considerable variability in the post-vaginal plate of *ridingsana*, no examples seemed to approach *griselda*. Figs. 12 and 13 show imagines of *ridingsana*, which will serve to illustrate the differences in maculation described above. The name for the new species is taken from Boccaccio's heroine, Griselda.

Eucosma salaciana A. Blanchard & E. Knudson, **new species**

Head: Palpi exceeding front by at least 1½ eye diameters. Second segment brushlike, with long dark brown scales on ventral aspect. Palpi otherwise yellowish brown. Front and Vertex yellowish brown. Antennae simple, yellowish brown.
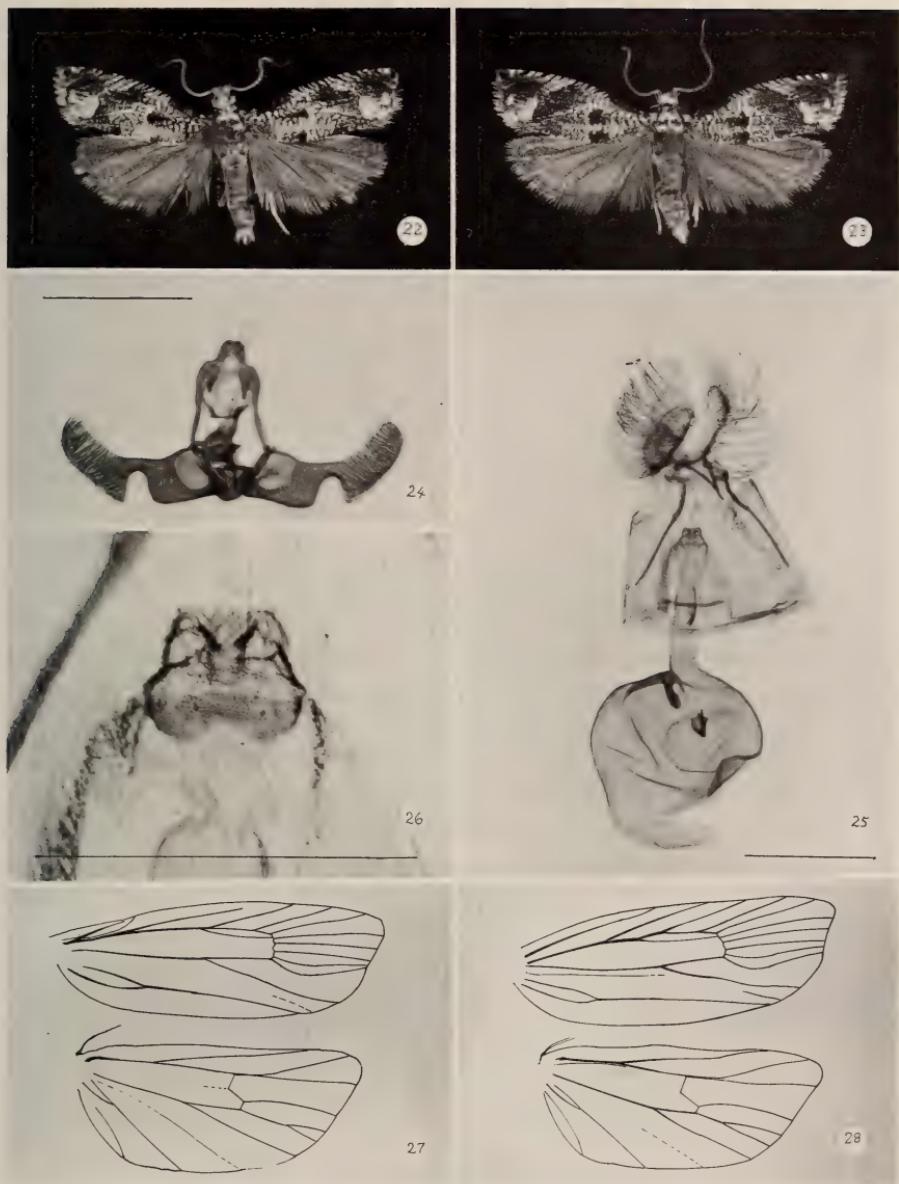
FIGS. 22–28. *Eucosma salaciana*; **22,** holotype male, North Padre Island, Nueces Co., Texas, 13-X-79, A. & M. E. Blanchard coll.; **23,** paratype female, same data as Fig. 22; **24,** male genitalia, paratype, slide E.C.K. 163, North Padre Island, Nueces Co., Texas, 12-X-79, E. Knudson coll.; **25,** female genitalia, paratype, slide E.C.K. 167, same data as Fig. 24; **26,** enlargement of sterigma from specimen in Fig. 23; **27,** male wing venation, paratype, slide A.B. 4977, North Padre Island, Nueces Co., Texas, 24-IX-79, A. & M. E. Blanchard coll.; **28,** female wing venation, paratype, slide A.B. 4983, same data as Fig. 22. (Line scales on Figs. 24, 25 represent 1 mm; Fig. 26 equals 0.5 mm.)

Thorax: Tegulae and mesonotum transversally banded with dark brown and creamy white.

Abdomen: Light grayish brown.

Forewing (Figs. 22, 23): Costal fold broad, flatly appressed, not extending beyond basal third of costa. Ground color creamy white, heavily overlain with dark brownish gray scales. Prominent dark brown blotch along the dorsal margin ⅓ the distance from base, extending to mid disc and interrupted by a narrow streak of ground color along the fold. A much smaller dark brown spot lies along the dorsal margin ⅔ the distance from base. An ill defined dark brown fascia extends from dorsal margin just basad of the ocelloid patch, angled inward toward the mid costa. Ocelloid patch prominent, pinkish white, with 1 to 3 narrow horizontal blackish dashes along the outer third. Costal margin heavily strigulated with creamy white and dark brown. Fringe whitish.

Hindwing (Figs. 22, 23): Smokey grayish brown with lighter fringe.

Length of forewing: *Males:* (N = 28), 5.7–7.8 mm, average 7.1 mm. *Females:* (N = 16), 6.3–8.3 mm, average 7.7 mm.

Venation (Figs. 27, 28): *Forewing:* Veins M2, M3, and Cu1 converging towards termen. *Hindwing:* Veins M3 and Cu1 anastamosing from ⅓ to ⅔ the distance to cell. Rs and M1 approximate towards base.

Male genitalia (Fig. 24): Slide ECK 163, from paratype, North Padre Island, Nueces Co., Texas, 12-X-79.

Female genitalia (Figs. 25, 26): Slide ECK 167, from paratype, North Padre Island, Nueces Co., Texas, 12-X-79. Fig. 25 is of entire genitalia, showing the large hairy ovipositor lobes. The ductus seminalis originates from the caudal third of the ductus bursae. Fig. 26 is an enlargement of the sterigma from the same slide.

Holotype (Fig. 22): Male, North Padre Island, Nueces Co., Texas, 13-X-79, collected by A. & M. E. Blanchard, deposited in the U.S. National Museum of Natural History (NMNH).

Paratypes: Eagle Lake, Colorado Co., Texas, 27-IV-78, 1 male, North Padre Island, Nueces Co., Texas, 24-IX-79, 9 males, 3 females, same locality, 13-X-79, 7 males, 9 females, all collected by A. & M. E. Blanchard. Same locality, 12-X-79, 12 males, 6 females, collected by E. Knudson.

Remarks

Eucosma salaciana has a wing pattern having many features in common with a sizeable group of species in the genus. Although not obviously separable by pattern from some of the other members of this group, this species is separated easily by the male genitalia, which is completely unlike all others in this pattern group. It is further separated from those species of *Eucosma* with a somewhat similar male genitalia by differences in the costal fold. The name of the new species is taken from Salacia, wife of Neptune and goddess of the sea in roman mythology.

Acknowledgements

Literature Cited

Heinrich, Carl. 1923. Revision of the North American Moths of the subfamily Eucosminae of the family Olethreutidae, U.S.N.M. Bulletin 123, Washington, D.C., pp. 71–136.

THE DAKOTA SKIPPER, *HESPERIA DACOTAE* (SKINNER): RANGE AND BIOLOGY, WITH SPECIAL REFERENCE TO NORTH DAKOTA[1]

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ABSTRACT. *Hesperia dacotae* (Skinner) (Lepidoptera: Hesperiidae) biology, ecology, behavior, and distribution have been examined in North Dakota and correlated with information from the remainder of the species' range. The skipper is oligolectic, utilizing *Ratibida columnifera* (Nutt.) and *Erigeron strigosus* Muhl. (both Asteraceae) with greatest frequency. The skipper requires calcareous prairie conditions and has niche requirements similar to that of the lily, *Zigadenus elegans* Pursh, although its life history is completely independent of the plant. The skipper appears to require a range of precipitation-evaporation ratios between 60 and 105 and a soil pH between 7.2 and 7.8. The larva is described and illustrated. The normal overwintering stage is probably the fourth instar larva.

Hesperia dacotae (Skinner) is a northern Great Plains species associated with calcareous (alkaline) prairies. These prairies are poorly suited for most agricultural purposes and usually serve as hayland or pasture. Calcareous prairies are of a fragile nature and even carefully controlled grazing rapidly alters the flora through soil impaction and selective feeding, making it unsuitable for the skipper.

Habitat destruction, through intensive agriculture or grazing, has so restricted the species' range that it has been proposed for Endangered Species consideration. The Water and Power Resources Service (formerly the Reclamation Bureau) needed a survey for the Dakota skipper to ensure no habitat would be lost as a result of the Garrison Diversion Project. This paper is derived from a report submitted to the Water and Power Resources Service, Bismarck, North Dakota. Garrison Diversion Units (GDU's) were intensively surveyed, but much of North Dakota was visited during the course of this study.

METHODS

The GDU's were initially surveyed by airplane. This was necessary as the entire flight span of the adult skipper is a brief 3–4 weeks. From the air it was possible to eliminate areas that showed no potential, i.e., areas under cultivation and overgrazed sites. Each portion of the GDU (see Fig. 7) was criss-crossed every four miles by plane. The main advantage of the aerial survey was to define the portion of the GDU which required an "on-the-ground" examination.

Potential habitat discovered by the aerial survey was marked on a map, and I visited each of these sites at least once. Potential sites included areas that have obviously been used for hay (hay bales still present) or were ungrazed and usually had gravel pits nearby (indicators of required gravelly subsurface conditions). These general requirements were based on observations I have made since 1968 on several North Dakota and Minnesota populations of the Dakota skipper.

The ground survey was accomplished between 8 July and 25 July 1979. These dates represent the flight period of the skipper for 1979 only. Over the years I have observed a range of flight periods beginning as late as 8 July or as early as 16 June. 1979's emergence date was established by watching an extant colony, the Felton prairie, Clay Co., Minnesota, every sunny day until the skipper began flying (Fig. 9). Once the flight period began, all GDU's not subjected to cultivation were traversed by automobile. This allowed for surveillance of considerably more territory than just the GDU's as much of eastern North Dakota was crossed while in transit. All likely sites, as viewed from the road or from the plane, were covered on foot and prevalent plants and animals were recorded. Each general area of the GDU (see map, Fig. 7) was visited three times. Persistent overcast conditions in the Oakes region (southeastern North Dakota) necessitated additional visits and even then conditions were not as ideal as is desirable. However, practically no suitable habitat was available and only one colony was discovered. Immediately south of Oakes, in South Dakota, considerable habitat is available and this area shows more promise than past records indicate.

BIOLOGY OF *HESPERIA DACOTAE*

Dakota skipper adults fly in June and July, and early spring climatic conditions determine their emergence date. Both sexes emerge on the same day. Mating takes place as early as the first day of emergence and both sexes will mate more than once. Females continue to lay eggs throughout their adult life, which is estimated at two–four weeks in nature. Eggs require 7–20 days to hatch, depending on temperature, with 10 days being typical. Eggs are laid on any broad surface with some preference given to broad-leaved plants, especially *Astragalus* spp. Grasses have not been observed to be used for oviposition sites.

The newly eclosed larva climbs down to the ground and webs two blades of grass together at ground level. *Poa pratensis* L., *Koehleria cristata* (L.) Pers., *Andropogon gerardi* Vitman, *Stipa spartea* Trin., *Phleum pratense* L., and *Carex* sp. were all accepted by confined first

instar larvae. Bunch grasses are preferred by *Hesperia* larvae, according to MacNeill (1964).

An older larva builds a silken tube lined with several blades of grass, enlarging it as the larva grows. Larvae seldom completely leave their tube, and feed mostly at night. The usual overwintering stage appears to be the fourth instar larva as determined by nearly a month's cessation of feeding in 8 of 10 larvae of this instar from one brood. Approximately 72 days, when the temperature reaches or exceeds 50°F, are required for the overwintering larva to develop to the adult stage.

The fully grown larva has a white patch on the venter of abdominal segments 7 & 8. This patch is comprised of a waxy hydrofuge substance produced by simple one-celled glands on the epidermis of the venter of the abdomen (Dethier, 1942). When the larva pupates, its turning action distributes this wax throughout and probably protects the pupa from excess moisture (MacNeill, 1964). High humidity is an important limiting factor on the survival of the skipper. A bacterial septicemia is known to kill *Hesperia* larvae held under humid conditions (MacNeill, 1964).

Dakota skipper larvae can be distinguished from all other described *Hesperia* larvae by the presence of pits on the ventral part of the head capsule. All other known *Hesperia* larvae have some portion of the lower face unpitted. The following description is based on ultimate instar larvae, but is supplemented, as indicated, with notes on earlier instars. I have used MacNeill's (1964) "ring-pores" for the peculiar plates of unknown function that appear on the integument. In addition, there are other ring-pore-like structures that are much smaller and lack the conspicuous inner plate of the ring-pore. I refer to these as rudimentary ring-pores. These are sometimes setigerous. Occasionally setae replace ring-pores on the thoracic segments of some larvae.

DESCRIPTION OF MATURE LARVA

General (Fig. 1): Head 2.80–3.00 mm wide. Total length 19.0–22.0 mm (N = 3). Abdominal prolegs present on third through sixth segments. *Crochets* multiordinal in a ring. *Anal comb* with 14–16 teeth. Head pitted throughout. Head and body with numerous short secondary setae, those on body blunt-tipped and probably glandular (Lindsey, 1923). Integument minutely granular (30 granules per 0.025 mm²). Spiracle T1 0.33 mm high and spiracle A8 0.28 mm high. Primary abdominal setae absent. Sclerotized portion of thoracic legs spiny, claws notched at base.

Coloration (living material): Head, prothoracic shield, thoracic legs, and spiracles black. Body light brown, flesh-colored. Venter of A7 and A8 covered with white wax in the ultimate instar larva.

Head (Fig. 3): Epicranial suture 0.90 mm long. Height of frons 1.52 mm. Adfrontal puncture (Afa) present as figured. Adfrontal seta apparently absent or not differentiated from numerous secondary setae. Lightly pigmented areas near vertex along epicranial
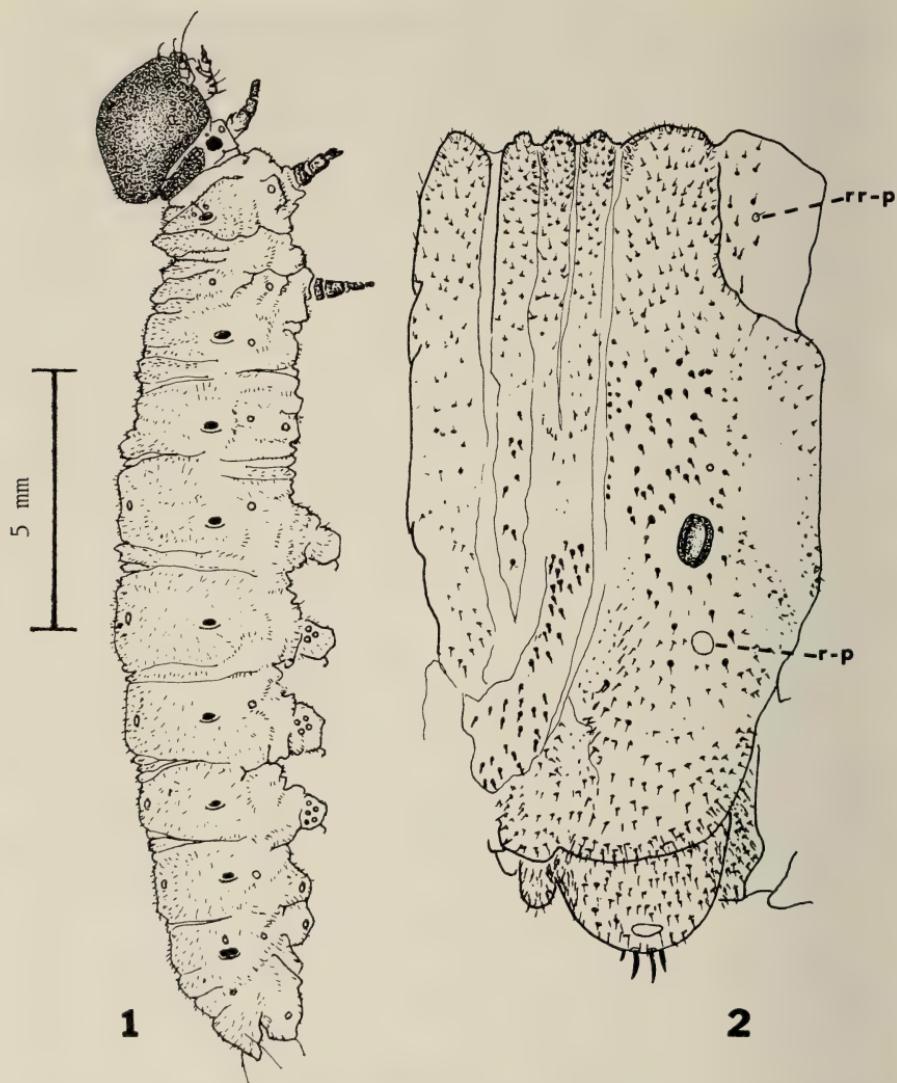
FIGS. 1 & 2.   1, Sixth instar larvae of *Hesperia dacotae* from Felton, Clay Co., Minnesota. 2, First abdominal segment of sixth instar larvae of *Hesperia dacotae*. rr-p, rudimentary ring-pore; r-p, ring-pore.

suture, between frontal and adfrontal sutures, on middle of frons, and on lower face as drawn. Ring-pores present at apex of dorsal pale area, one just above Oc-6, and a third directly above that, about midway up the head capsule. *Mouthparts:* Hypopharyngeal complex (Fig. 6): Spinneret much shorter than labial palpi, apex wedge-shaped and bare; proximal three-fourths of hypopharynx covered with fine spines; prementum with a notch in dorsal apex; basal segment of labial palpus with apical seta equal to twice the length of apical segment of palpus; apical segment with a short seta. Mandible
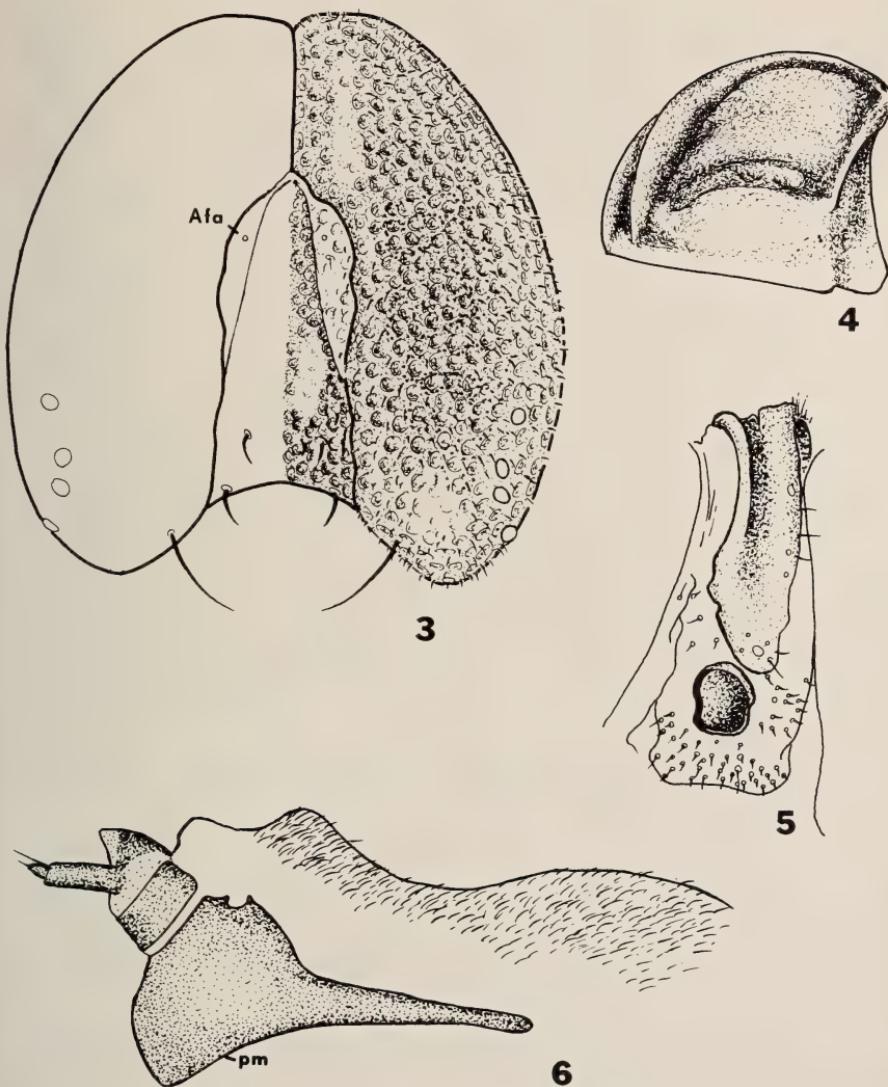
FIGS. 3–6. **3,** Head capsule of sixth instar larvae. **Afa,** adfrontal puncture. **4,** Oral aspect of left mandible. **5,** First thoracic segment illustrating shield. **6,** Hypopharyngeal complex. **pm,** prementum.

(Fig. 4): Simple, lacking inner ridges or teeth, with a slight concavity near middle of oral face.

Thoracic segments: *Prothorax:* Cervical shield (Fig. 5) is subdivided in penultimate 6th instar larvae and in earlier instars, forming a second sclerite or subshield between the dorsal portion of the shield and the spiracle. Shield with a ring-pore along anterior margin of subdorsal region and at lateral apex. A primary seta, when present, replaces the lateral ring-pore of the shield. Shield with a transverse groove and a row of anterior
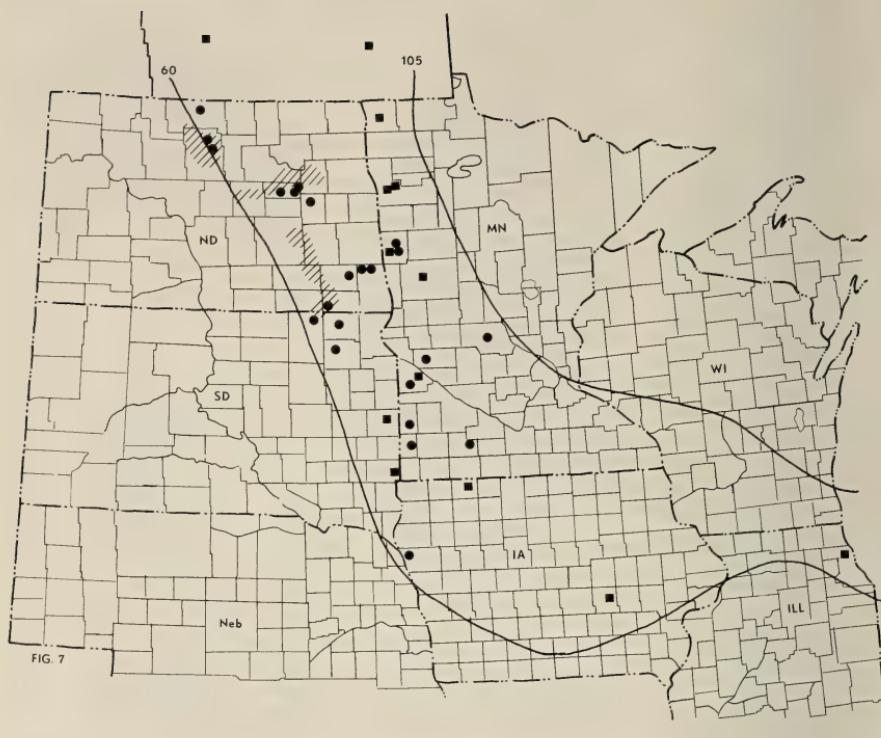
FIG. 7.   Recent ● and historical ■ records for *Hesperia dacotae*. ———— Precipitation-evaporation ratios (after Transeau, 1905). ///// Garrison Diversion Units.

setae. Ring-pore present anterodorsal to coxal base. *Mesothorax* with simple, long, primary seta located midlaterally, just dorsal to line of abdominal spiracles. 2, 1, or 0 ring-pores present dorsal to this seta. Single sublateral ring-pore present. *Metathorax* with ring-pore present in line with mesothoracic seta and dorsal to line of abdominal spiracles. A second dorsal ring-pore present in penultimate instars, but absent in ultimate instar larvae. A single sublateral ring-pore present.

Abdominal segments (Fig. 2): *Ab-1&2:* Dorsal ring-pore present; lateral ring-pore present or absent, if present located posterior to line of spiracle; sublateral ring-pore, positioned below spiracle, present or absent, when present anterior or posterior to line of spiracle; ventral ring-pore present. Also a rudimentary ring-pore (sometimes setigerous) located dorsal to spiracle at about the distance of the diameter of the spiracle. Another rudimentary ring-pore present subdorsally on the anterior edge of the segment. *Ab-3:* Dorsal ring-pore present; lateral ring-pore present or absent; sublateral ring-pore present, anterior or posterior to vertical line of spiracle; ventral ring-pore absent; rudimentary ring-pore present anterodorsal to spiracle and subdorsal rudimentary ring-pore present in same position as that of Ab-1&2. *Ab-4:* Same as Ab-3 except 3–5 ring-pores present on each proleg. *Ab-5:* Same as Ab-3 except 3–7 ring-pores present on each proleg. *Ab-6:* Same as Ab-5. *Ab-7:* With dorsal ring-pore present; lateral ring-pore present or absent; sublateral and ventral ring-pores present. *Ab-8:* Lateral rudimentary ring-pore now anterior to and in line with the spiracle and less than one-half the diameter of the spiracle in distance from it. Subdorsal rudimentary ring-pore present and in same location as on Ab-3. Dorsal, lateral, and ventral ring-pore all present. *Ab-*

9: With dorsal, subdorsal, lateral and ventral ring-pores present or absent in any combination. *Ab-10:* With ventral ring-pore present. *Suranal plate:* Numerous pigment spots present on anterior margin of segment, varying in shape, number, and position.

Material examined: 3 sixth (ultimate) instar larvae, 1 sixth (penultimate) instar larva, and 3 fifth instar larvae, all reared from ova from a female collected at Felton prairie, lat. 47.03.44 long. 96.26.00 (T142N R45W S6), Clay Co., Minnesota. Larvae preserved 8 October 1979 and 15 September 1979. All larvae, P1♀, and 3 F1's are coded tlm 79-49. Duplicate specimens are deposited in the New York State Museum.

Courtship

Females are initially encountered by males during routine territorial skirmishes. Any female flying within the visual range of the male is approached. The female promptly moves away a short distance and then alights. Inevitably, the male pursues the female to this point and lands below the female and climbs to a side-by-side position. This is done without the vibrating of the wings MacNeill (1964) observed in other species of *Hesperia*. The male curls the abdomen under and to the side and attempts to copulate with the female. If the female is receptive, she extends her ovipositor and they mate.

It is apparent in this species that the female has to be receptive to ensure mating. Males attempted to mate with females of their own species or with those of the sympatric *Polites themistocles* (Latreille). The female determined if the male was acceptable. This is in contradiction to what MacNeill (1964) reported for other species of *Hesperia*. I have observed intergeneric and even interfamilial mating attempts in other species of skippers, notably between a male *Epargyreus clarus* (Cramer) and a female *Megathymus streckeri texanus* B. & McD., and in my experience it is the female that determines the successful copulation.

Frequently the female rejects the first few advances of the male. The male eventually loses interest and leaves. Within a minute or two thereafter, the female will fly off and reach a new perch to bask, feed, or oviposit. If the male is unsuccessful in his first attempt to mate, he may rest alongside the female for a few minutes. Frequently he places both forelegs on the costa of the forewing of the female while resting. Female displacement behavior, during this time, consists of antennal grooming. Normally after a male loses interest in an unreceptive female, he flies to a nectar source and feeds (displacement activity) before resuming territorial perching. Total duration of a successful mating has not been recorded, although one pair was observed to mate and was still copulating 45 minutes later, but the pair had moved by the time the site was revisited after 60 minutes.

Territorial (used here to indicate intraspecific aggression) males frequently encounter one another leading to typically brief skirmishes, characterized by whirling, ascending flight. Both males involved often

return to their original vantage point, usually a tall plant or an open area, and encounter each other repeatedly.

Submissive flight by males has been observed. This type of flight can be recognized by the lower pitch of the wings and the slower wing beat. Submissive males appear to be mistaken for females. On many occasions, three or four males have been observed pursuing a submissive male in a flight pattern reminiscent of males following females. The submissive male typically appeared to be larger than the aggressors. Several submissive males were captured and examined to eliminate the possibility of the presence of the similar and sometimes sympatric *Hesperia ottoe* Edwards. When the submissive male alights, the pursuing males quickly lose interest and return to their territorial sites.

ECOLOGY

I have observed the Felton prairie, Clay Co., Minnesota, for a number of years and have noticed a yearly shift of the Dakota skipper's main activity center (territoriality, oviposition, and mating) each year. Such movement may be an effect of contour (skipper usually seeks high vantage point), wind (skipper gathers on windward side of prairie), nectar sources, or edaphic conditions. Only one North Dakota site, the Karlsruhe prairie (Fig. 10), was large enough to support separate demes. A "walk-through"* count of 26 ♂♂ and 4 ♀♀ probably represents a mere tenth of one aggregation site, and as there were at least eight other widely separated aggregations noted on the Karlsruhe prairie, the overall population may run into the thousands. This may be the only population where deme interaction or deme size can be studied. All other known sites are so small that the population functions as a single deme.

Captured specimens of the Dakota skipper typically fly 150–200 feet when released and then settle down in the grasses. After a few minutes, the skipper begins to fly back to the vicinity of where it was disturbed, usually in 50 foot stages. Mark-recapture studies should work quite well with this species, but were not attempted because of time limitations. It is of interest that the skipper flew out of visual range of one observer. With two observers, one stationed directly downwind (the usual direction of escape flight) 150 feet, it was very easy to locate an individual on alighting. With only one observer, visual tracking was possible for less than 100 feet. This may be similar to the capabilities of a vertebrate predator, notably a bird, and might

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* All sightings during two parallel walks, 50 feet apart, through what appears to be the main concentration of activity.

FIG. 8.   Nectar sources for *Hesperia dacotae*
(given in order of preference).[1]

Ratibida columnifera (Nutt.)	[Asteraceae]
Erigeron strigosus Muhl.	[Asteraceae]
Echinacea angustifolia (DC.) Heller	[Asteraceae]
Gaillardia aristata Pursh	[Asteraceae]
Rudbeckia serotina Nutt.	[Asteraceae]
Campanula rotundifolia L.	[Campanulaceae]
Oenothera serrulata Nutt.	[Onagraceae]

UNACCEPTABLE NECTAR SOURCES[2]

Asclepias ovalifolia Dec.	[Asclepiadaceae]
Apocynum sibiricum L.	[Apocynaceae]
Asclepias syriaca L.	[Asclepiadaceae]
Galium boreale L.	[Rubiaceae]
Lilium philadelphicum L.	[Liliaceae]
Petalostemum candidum Michx.	[Fabaceae]
Spiraea alba DurRoi	[Rosaceae]

[1] Based on number of sighting of feeding adults.
[2] Available at most sites, but not used by skipper.

explain why the skipper flies 150 feet and not 50 or 100 before alighting.

Year to year population peaks and declines have not been reported for the Dakota skipper. Sites I have visited repeatedly (since 1968) have a population that appears to be very stable. A decline appeared on the Felton prairie in 1975 when the prairie was hayed in June, but this was a result of emigration of the adults in search of nectar sources. Some mating and oviposition must have occurred on the first day or two from emergence to account for the quick rebound of the population (numbers were back to normal in 1977). A yearly June mowing would be highly detrimental. The Felton prairie is normally hayed in September, and then, not every year.

Interspecific competition does not appear to be the limiting factor of *H. dacotae* distribution. Other species commonly found on or near *H. dacotae* sites, and which have adults occurring at the same time, use dogbane and milkweed blossoms most frequently. These nectar sources are not used by *H. dacotae* (see Fig. 8). Only three attempted interspecific (and intergeneric) matings were observed and these were all between *Polites themistocles* females and *H. dacotae* males. In these instances, the male pursued the female until she rested and the male attempted to copulate, but the female was not receptive.

Actual predation on *H. dacotae* has been observed only from three groups: Ambush bugs (Hemiptera: Phymatidae; *Phymata* sp.), flower spiders (Aranaea: Thomisidae; *Misumena vatia* (Clerck)), and orb weavers (various Aranaea). The first two predators are cryptically colored to match flowers and are commonly found on *Ratibida colum-*

FIG. 9.   Early season succession of prairie plants and butterflies.[1]

Date	Plant species[2]	Butterfly species—first noted and condition
16 June	*Oxalis violacea* L. *Lithospermum canescens* Michx. *Viola pedatifida* G. Don *Commandra pallida* A. DC.	*Chlosyne gorgone carlotta* (Reakirt)—worn ♂'s *Atrytonopsis hianna* (Scudder) —worn ♂'s, fresh ♀'s *Oeneis uhleri varuna* (Edw.) —worn ♂'s, fresh ♀'s
26 June	*Gaillardia aristata* Pursh* *Galium boreale* L.	*A. hianna*—worn ♀'s *O. u. varuna*—worn ♀'s *Lycaeides melissa* (Edw.) —fresh ♂'s *Coenonympha tullia benjamini* McD.—fresh adults
30 June	*Asclepias ovalifolia* Dec. *Onosmodium occidentale* Mackenz. *Psoralea esculenta* Pursh *Zigadenus elegans* Pursh *Erigeron strigosus* Muhl.* *Lilium philadelphicum* L.	*L. melissa*—fresh ♀'s *Polites themistocles* (Latr.) —fresh adults *A. hianna*—very worn
4 July	*Campanula rotundifolia* L.* *Oenothera serrulata* Nutt.*	*Polites mystic decotah* (Edw.) —fresh ♂'s *P. themistocles*—fresh adults
8 July[3]	*Petalostemum candidum* Michx. *Senecio plattensis* Nutt. *Ratibida columnifera* (Nutt.)*	*Hesperia dacotae* (Skinner) —fresh adults *Oarisma powesheik* (Parker) —fresh adults

[1] Succession study done in 1979 on the Felton prairie, Clay Co., Minnesota.
[2] The date the first opened blossoms were recorded; plants continued to bloom through skipper flight period in most cases.
[3] *Echinacea angustifolia* was still not in bloom although it occurs on the site and later in the season is an important nectar source.
* Flowers served as nectar sources for *Hesperia dacotae*.

nifera (Nutt.) and *Erigeron strigosus* Muhl., respectively. They are very effective predators of any nectar feeding insect. One of the chief nectar sources of *H. dacotae*, harebell (*Campanula rotundifolia* L.), is not utilized by flower spiders or ambush bugs. Orb weaver spiders appear to be successful only with old, worn individuals. Fresh active adults manage to quickly break from the webbing because they have an abundant supply of loose scales.

Many *H. dacotae* sites have numerous dragonflies, chiefly gomphids and libellulids. Despite many hours of observation, no dragonfly or bird predation was observed. Egg parasites have been reported for *Hesperia lindseyi* (Holland) (MacNeill, 1964) and a braconid larval parasite has been reported for *H. comma assiniboia* (Lyman) (McCabe & Post, 1977). The most important mortality factor appears to be the bacterial septicemia reported by MacNeill (1964).

FIG. 10.   North Dakota Localities for *Hesperia dacotae.*

Site	Township-range-section	County	Approx. acreage
Karlsruhe	T154N R76W S20, 28–30	McHenry	1500
McLeod	T134N R53W S8	Ransom	100
Binford	T147N R60W S16	Griggs	150
Spring Creek	T149N R62W S22	Eddy	100
Oakes	T130N R58W S17, 18	Sargent	600
Towner	T157N R76W S17	McHenry	6
New Rockford	T149N R65W S29	Eddy	120
Hamar 1st	T150N R62W S23	Eddy	300
Hamar 2nd	T150N R62W S15	Eddy	40
Bottineau	T162N R76W S12	Bottineau	100
Colvin prairie	T149N R62W S32	Eddy	4
Kindred	T136N R51W S24	Richland	30
Walcott	T136N R51W S35	Richland	400

Alkaline prairies, required by the skipper, are poor soils and not desirable for cultivation. These soils are frequently used for pasturing cattle or for hay. Despite the existence of numerous such grazed prairies in North Dakota, only one grazed site, New Rockford (Fig. 10), had any *H. dacotae,* and this may have been the remains of a former population, as it was obvious that the prairie had only recently been converted to grazing. Through their movements, cattle may be physically destroying the larvae, although certain species of skippers, such as *H. comma assiniboia,* are able to tolerate grazing (McCabe & Post, 1977). The oligolectic habits of adult Dakota skippers, combined with the effect of grazing, may prohibit occupancy of both cattle and skipper. Tooth-leaved primrose, *Oenothera serrulata* Nutt., and harebell succumb rapidly before even light grazing pressure. Long-headed coneflower, *Ratibida columnifera* (Nutt.), and purple coneflower, *Echinacea angustifolia* (DC.) Heller, do a little better, but are eliminated by overgrazing. The very productive nectaries of milkweeds and dogbanes, generally avoided by grazers, are not utilized by the Dakota skipper. Other species of flowers will undoubtedly be used by the skipper as they become available in parts of the species' range.

Since Dakota skipper larvae are general feeders on grasses, one needs to look beyond a simple host requirement to determine why a particular prairie is acceptable habitat. Larvae make vertical, elongate, silk-lined tubes at the surface of the ground. Soil pH and humidity factors may be of importance to larval survival. Most Dakota skipper sites have standing water in the surrounding ditches, indicating probable periodic high humid conditions at ground level, despite the gravelly subsurface soils. Soil pH has proved to be an important factor in terms of survival in some skipper species. Freeman

(1964) found that one megathymid skipper had a pH tolerance range of less than 0.2. The white ladyslipper, *Cypripedium candidum* Willd., frequently found on *H. dacotae* sites, requires a soil pH of 7.2–7.8 (Sheviak, 1974). Prairie fringed orchid, *Habenaria leucophaea* (Nutt.) Gray, and wild lily, *Lilium philadelphicum* L., also calciphiles, are typically found on these prairies. Camas, also known as "alkali grass," *Zigadenus elegans* Pursh, another calciphile, was found everywhere the Dakota skipper occurred and the converse was true with rare exception. At no stage is the skipper dependent on camas, and it is just coincidence that both species have similar habitat requirements. The occurrence of the skipper and camas together outside of North Dakota has not been studied. Camas is much easier to detect than the skipper, and, as an added feature, camas blossoms' development and senescence closely approximates that of the flight period of the adult skipper. Camas, at least in North Dakota, is an extremely reliable indicator of Dakota skipper habitat.

Grassland used for hay is normally mowed before *Stipa* grasses produce seed or else after seed drop. *Stipa* grass seeds are barbed and will stick in an animal and subsequently benefit from active animal transport. Cattle can be injured when the ripe seeds penetrate the mouth, hence these grasses must be harvested early or late in the season if they are to be used for cattle feed. The seeds are formed almost the same time the skipper begins to fly. Pre-seed harvesting destroys nectar sources for the adult skipper and forces the skipper to emigrate in search of nectar.

The ideal maintenance of Dakota skipper prairies consists of late-season mowing, a practice that can easily be arranged with local farmers on publicly owned lands. Late-season haying provides the best cover for ground-nesting birds and is also the preferred treatment for prairie orchids. Curtis (1946) studied the white ladyslipper which had been continually losing ground on the University of Wisconsin arboretum. With either early spring (April in Wisconsin) or late-season mowing, Curtis was able to double orchid production. In the historical past, periodic grazing by buffalo and occasional prairie fires may have maintained the habitat, but it is likely that the adult skipper was forced to seek new locations under these circumstances. As much habitat was suitable during this period, a migration and recolonization effort was feasible. Under present extensive agricultural practices, suitable habitats have been reduced to widely separated "islands," virtually eliminating any successful recolonization attempts.

Burning is probably not a cure-all for the skipper. A June through early July burn would destroy the eggs which are on exposed vegetation. Diapausing fourth instar larvae may be destroyed if ground

level heat reaches a critical point. Susceptibility of adults or larvae to burns is not known. A burn at night would very likely destroy the adults and a slow back-burn may destroy any larval stage, not to mention the loss of nectar sources and depletion of nitrogen.

Prairies that are "preserved" from all activities show rapid plant succession and result in an undesirable growth of woody shrubs. I witnessed this transition on a prairie south of Buffalo State Park, Clay Co., Minnesota. Ownership of the prairie changed and it was no longer cut for hay. Public opinion prevented burning at the time and willows and horsetails began to dominate many sections. Finally, a controlled burn was performed, but several species, including *Hesperia comma*, have not been taken there since. I do not know which practice, lack of haying or the burn, eliminated the skipper.

A late-season mowing that is timed to the best advantage of prairie flowers, ground-nesting birds, and the Dakota skipper is needed. A very late (October) mowing is optimal. Any attempt at a burn should be done with the knowledge of the location of the previous season's main oviposition sites and these sites should be sheltered from the burn. I am aware of a Dakota skipper prairie (Hook & Bullet Refuge, lat. 46.48.21, long. 96.23.38, Clay Co., Minnesota) that has been maintained by mowing for more than 50 years.

HISTORICAL PERSPECTIVE AND DISTRIBUTION

The Dakota skipper was described in 1911 by H. Skinner from a series of adults collected at Volga, South Dakota by Dr. Truman and from Grinnell, Iowa, presumably collected by Parker. Holland (1931) figured a paratype. Lindsey et al. (1931) gave additional records for Sioux City, Iowa. Lindsey (1942) gave records for Miniota, Manitoba; Lake West Okoboji, Iowa, and remembered seeing specimens from the Chicago area. Irwin & Downey (1973) reported three specimens of *H. dacotae* in the Carnegie Museum that were labeled Illinois. I visited the Carnegie Museum, where I was able to examine the holotype of *H. dacotae* and also dissected a specimen labeled "Ridgeland, Ill." (now a part of Chicago) which proved to be a *H. dacotae*. It was last recorded in Illinois in 1888. Macy & Shepard (1941) give the additional localities of Winnipeg, Manitoba; Gentilly, Polk Co., Madison, Lac Que Parle Co., and Kittson Co., Minnesota. Nordin (1967) gave records for Brown Co., South Dakota. Hooper (1973) mentions Brandon, Manitoba and McCabe & Post (1977) give records for Bottineau, Richland, and Ransom Counties, North Dakota. Nordin (pers. comm.) adds Day and Marshall Counties, South Dakota and Downey has taken it in Woodbury Co., Iowa (pers. comm., R. L. Huber). Huber (pers. comm.) has taken it in Pipestone and Cottonwood

Counties, Minnesota and both Huber and Dana have it from Lincoln Co., Minnesota. Dana and Muggle have recorded it from Stearns Co., Minnesota (pers. comm., R. Dana). Numerous people have recorded it from the Felton prairie, Clay Co., Minnesota.

There appears to be a correlation between precipitation-evaporation ratios and skipper distribution (Fig. 7). This is supported by present known distribution and biological inferences that are based on mortality factors and habitat requirements. Only a small portion of the overall area circumscribed by the precipitation-evaporation ratios of 60 to 105 (Transeau, 1905) is suitable for colonization by the skipper. Within this narrow belt the species needs to have proper edaphic conditions and suitable nectar sources. Lake Michigan possibly served as a physical barrier to the eastern extension of the species' range. Northern limits have not been established because of the lack of records from Manitoba.

McCabe & Post (1977) reported ". . . *dacotae* is associated with the shorelines of glacial lakes . . . Agassiz and Souris in our area." Even with additional records from the present study, this still appears to be the case in North Dakota. The east-central North Dakota records are on the shores of Glacial Devil's Lake (see Lemke et al., 1965, for map of glacial lakes) and the southernmost North Dakota record and northeastern South Dakota records are on the shores of Glacial Lake Dakota. More southerly records, however, show no correlation to glacial lakes with the exception of the single Illinois record (Glacial Lake Chicago).

Glacial lake shorelines are frequently alkaline. The skipper's apparent pH requirements may mean that shores are good habitats. In addition, the gravelly shores are poor for most agricultural purposes and are spared from cultivation. After the retreat of the Wisconsinan glaciers, the species may have pushed northward, and presently occurs only on shorelines because of the loss of suitable habitat elsewhere. Climatic factors, particularly precipitation-evaporation ratios, and edaphic factors in conjunction with present agricultural practice, may account for the distribution. Conversely, the skipper may have been a "shore species" during the time of the glacial lakes, and has failed to expand its range since the lakes were drained (7500–12,500 years before present for Glacial Lake Agassiz (Flint, 1971)).

indebted to Mr. Ron Huber for encouragement and counsel early in my study of skippers and much correspondence over the years on *Hesperia dacotae* and other species. I thank Carol Teale for the illustrations.

LITERATURE CITED

CURTIS, J. T. 1946. Use of mowing in management of White Ladyslipper. Jour. Wildlife Man., 10(4): 303–308.

DETHIER, V. G. 1942. Abdominal glands of Hesperiinae. Jour. N.Y. Ent. Soc., 50(2): 203–206.

FLINT, R. F. 1971. Glacial and Quaternary Geology. John Wiley & Sons, Inc., New York, pp. 1–892.

FREEMAN, H. A. 1964. The effect of pH on the distribution of the Megathymidae. Jour. Res. Lep., 3: 1–4.

HOLLAND, W. J. 1931. The butterfly book. Doubleday & Co., Inc., Garden City, New York. 424 pp.

HOOPER, R. R. 1973. The butterflies of Saskatchewan. Saskatchewan Dept. Nat. Resources, Regina. 216 pp.

IRWIN, R. R. & J. C. DOWNEY. 1973. Annotated checklist of the butterflies of Illinois. Ill. Nat. Hist. Survey, Biol. Notes No. 81.

LEMKE, R. W., W. M. LAIRD, M. J. TIPTON & R. M. LINDVALL. 1965. Quaternary Geology of Northern Great Plains. *In* The Quaternary of the United States. Edited by H. E. Wright, Jr. and D. G. Frey. Princeton Univ. Press, pp. 15–27.

LINDSEY, A. W. 1923. The egg and larva of b4Hesperia juba Bdv. Denison Univ. Bull., Jour. Sci. Lab., 20: 121–125.

——— 1942. A preliminary revision of *Hesperia*. Denison Univ. Bull., Sci. Lab., Jour., 37(1/2): 1–50.

———, E. L. BELL & R. C. WILLIAMS, JR. 1931. The Hesperioidea of North America. Denison Univ. Bull., Sci. Lab., Jour., 36: 1–142.

MACNEILL, C. DON. 1964. The skippers of the genus *Hesperia* in western North America with special reference to California (Lepidoptera: Hesperiidae). Univ. of Calif. Public. in Ent., Vol. 35. 230 pp.

MACY, R. W. & H. H. SHEPARD. 1941. Butterflies, a handbook of the butterflies of the United States, complete for the region north of the Potomac and Ohio Rivers and east of the Dakotas. Minneapolis: Univ. Minnesota Press. 247 pp.

MCCABE, T. L. & R. L. POST. 1977. Skippers (Hesperioidea) of North Dakota. N.D.S.U. Agric. Exp. Sta., N. Dak. Insects, Public. No. 11. 70 pp.

NORDIN, J. S. 1967. 1966 Hesperiidae records for South Dakota. Minn. Assoc. Ent., Newsl., 1(4): 90–92.

SHEVIAK, C. 1974. An introduction to the ecology of the Illinois Orchidaceae. Ill. State Mus. Scient. Papers 14. 89 pp.

SKINNER, H. 1911. New species or subspecies of North American butterflies (Lepid.). Ent. News, 22(9): 412–413.

TRANSEAU, E. N. 1905. Forest centers of eastern North America. Amer. Nat., 39: 875–889.

A REVISION OF THE AGARISTID GENUS *AUCULA* WALKER (LEPIDOPTERA: NOCTUIDAE)

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ABSTRACT.   The neotropical agaristine genus *Aucula* Walker is revised. Twenty-four species are treated, of which 21 are described as new. The adults and the male genitalia of each species are illustrated, and the species are keyed on the basis of the male genitalia. Five species previously included in *Aucula* are transferred to other genera.

The purpose of this paper is to revise the genus *Aucula*. As treated here there are three previously described species and 21 new species. Five species previously included in *Aucula* are removed from the genus. The genus *Arpia* is removed from synonymy with *Aucula,* and the type species, *janeira* Schaus, is restored as *Arpia janeira* Schaus. *Bepara sublata* Walker is removed from *Aucula* and placed in *Darcetina* Felder, **Darcetina sublata** (Walker), **NEW COMBINATION**. Three species previously placed in *Aucula, Aucula schausi* Jorgensen, *Euthisanothia magnifica* Schaus, and *Metagarista hilzingeri* Berg are temporarily returned to or retained in their original genera but will eventually fall into a new genus John G. Franclemont plans to describe. Kiriakoff (1977) indicated that the senior author was planning a revision of *Aucula* and, therefore, followed the treatment of the genus used by earlier workers.

Only slightly over a hundred specimens of *Aucula* were found. The bulk of the specimens belong to a few species and many of the species are represented by unique specimens. We do not know why specimens are so rare in collections, but apparently they are not readily attracted to lights. Females are particularly scarce and are known for only a few species. Consequently, we have not attempted to describe the females of any species even when we were fairly certain females had been correctly associated with males. The foodplants are completely unknown. The genus *Aucula* is limited to South America except for one species which occurs in Panama. Most of the new species names are arbitrary combinations of letters and should be treated as feminine nouns. Because of the tremendous similarity of most of the species of *Aucula*, the descriptions are essentially comparative. We have described *Aucula hipia* new species in some detail and have used it as a basis from which to describe and compare most of the

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other species, rather than repeating essentially the same description for each species.

The authors wish to express their appreciation to John G. Franclemont, who not only initiated this study, but also thoroughly reviewed the original manuscript.

Aucula Walker, 1862, Trans. Ent. Soc. London 3(1): 253

Type-species: *Aucula josioides* Walker, 1862, *ibidem* 3(1): 253 monotypy.

Aucula is a superficially homogeneous group as defined in this paper. The wings are rounded in appearance and either a rich dark brown or rich red-brown. The two tropical American agaristid groups it might be confused with are *Gerra* Walker and *Darceta* Herrich-Schaeffer, 1856 (=*Diamuna* Walker, 1857 [1858]). The male genitalia of *Aucula*, despite a bewildering array of modifications, always lack a distinct median process of the sacculus or have the median process so modified as to be unrecognizable as such. The median process of the sacculus of the valve is present in all species of *Gerra* and *Darceta* examined and is never extremely modified. All species of *Gerra* examined have a distinct yellow patch at the base of the forewing below. In *Aucula* this patch is absent or only slightly present, never in the form of a distinct patch. The forewing of species of *Darceta* has a slightly falcate apex, but in *Aucula* the apex is evenly rounded and not falcate. A formal description of *Aucula* is given below.

Head: Antennae pectinate in both males and females, each pectination ciliated and tipped with a bristle; vestiture of head long red-brown scales, with a few intermixed white scales; weak tuft of scales from vertex projecting through antennal bases, but no other significant tufts; front completely scaled; front usually with tubercle or prong, its strength variable between species; distinct genae present, lower margin of front not flush with eyes; proboscis of normal development; palpi not reduced, third segment very short, globular, much shorter than second segment. **Thorax:** Dorsal surface covered with long red-brown hair-like scales; no distinct tufts except for suggestion of tuft at base of thorax; wing venation typical of subfamily (see Hampson, 1910, fig. 199); prothoracic, mesothoracic, and metathoracic legs with ventral surfaces of first four tarsal segments with long, irregularly spaced spines, not arranged in three distinct rows; fifth tarsal segment with strong lateral rows of spines, but only slightly hairy centrally; dorso-apical tip of fifth tarsal segment with four hair-like spines, two medially and two laterally; tarsal claws with strong apical tooth. **Tympanal region:** Tympanal membrane strongly recessed and enclosed posteriorly by moderately developed hood; sclerite nodular; alula moderately developed; tympanal groove strong, continued by distinct depression in anterior margin of second abdominal tergite; margin of first tergite distinctly emarginate, but not lipped at anterior of segment overhanging tympanal groove; distinct bulla-like structure in membrane posterior to hood. **Abdomen:** Males with basal hair pencils and accessory hair pencils; eighth male sternite without accessory rods or hair pencils; in females seventh sternite and tergite enlarged, modified, greatly sclerotized. **Male genitalia:** Variable with no consistent features; however median process of sacculus of valve absent, or if present, greatly modified; aedeagus short,

usually with apical projection; vesica without spines or cornuti. **Female genitalia:** Variable, ovipositor lobes long, apices elongate and slightly pointed at apex.

Key to the Species of *Aucula* Based on the Male Genitalia

1. Uncus very large, as broad as apical fifth of valve _____ 19
   Uncus reduced, slender or slightly enlarged apically, not as broad as apical fifth of valve _____ 2
2. Valve with clasper _____ 3
   Valve lacking clasper _____ 7
3. Clasper sinuous, several times as long as wide _____ 4
   Clasper straight, about twice as long as wide _____ *A. fona* n. sp.
4. Uncus reduced, minute; apex of clasper directed distad; apex of valve truncate, slightly concave _____ *A. psejoa* n. sp.
   Uncus not reduced; apex of clasper directed basad; apex of valve bluntly rounded or lobed at end of ventral margin _____ 5
5. Clasper large, length greater than width of valve; valve not lightly sclerotized or lobed at ventral margin _____ 6
   Clasper smaller, length distinctly less than width of valve; valve lightly sclerotized, lobed at apex of ventral margin _____ *A. lolua* n. sp.
6. Tegumen rounded, widest at middle, greatest width greater than greatest width of valve _____ *A. josioides* Walker
   Tegumen not rounded, not wider at middle, greatest width not greater than greatest width of valve _____ *A. munroei* n. sp.
7. Apex of valve sharp, pointed; apical patch of prominent black setae absent __ _____ *A. buprasium* (Druce)
   Apex of valve not sharp, pointed; apical patch of prominent black setae present _____ 8
8. Prominent black setae present on entire length of costal margin of valve or in patches at both base and apex of valve; apex of uncus slightly expanded 9
   Prominent black setae not present on basal part of costal margin of valve; apex of uncus not expanded _____ 12
9. Prominent black setae on entire length of costal margin of valve __ *A. byla* n. sp.
   Prominent black setae of costal margin of valve forming basal and apical patches _____ 10
10. Distance between patches of black setae of costal margin of valve greater than width of either patch _____ *A. dita* n. sp.
    Distance between patches of black setae of costal margin of valve less than width of either patch _____ 11
11. Ventral margin of valve slightly concave before apex; costal lobe of clavus clavate, greatest width shortly before apex _____ *A. usara* n. sp.
    Ventral margin of valve not concave before apex; costal lobe of clavus tapering to blunt point, widest near middle _____ *A. azecsa* n. sp.
12. Apex of valve truncate, apical margin slightly concave; costal margin of valve less than one-half greatest length of valve _____ *A. ceva* n. sp.
    Apex of valve not truncate, apical margin convex; costal margin of valve more than one-half greatest length of valve _____ 13
13. Costal margin of valve armed with large process near base _____ 14
    Costal margin of valve lacking basal process _____ 16
14. Costal margin of sacculus with a large sclerotized triangular process _____ 15
    Costal margin of sacculus simple, lacking processes _____ *A. tricuspis* Zerny
15. Length of process of base of costal margin of valve about 3 times as long as width of base of process; process of costal margin of sacculus as long as wide; large apical process of aedeagus scobinate _____ *A. gura* n. sp.
    Length of process of costal margin of valve about 5 times as long as width of base of process; process of costal margin of sacculus wider than long; large apical process of aedeagus glabrous, bifid _____ *A. hipia* n. sp.

16. Clavus an elongate, spatulate lobe, as long as width of valve; costal margin without prominent setae at middle; apex of valve with a large, dense ovoid patch of black setae extending obliquely to inner surface of valve at distal one-third _____ *A. exiva* n. sp.
    Clavus variably shaped, if a free lobe, not spatulate and not as long as width of valve; costal margin of valve with a marginal row of prominent black setae from middle to apex or at least at middle _____ 17

17. Posterior part of tegumen with strong, straight, spine-like setae; clavus with costal margin straight _____ *A. fernandezi* n. sp.
    Posterior part of tegumen without spines; clavus with costal margin concave, crescent-shaped _____ 18

18. Costal margin of clavus toothed medially _____ *A. sonura* n. sp.
    Costal margin of clavus not toothed medially _____ *A. nakia* n. sp.

19. Uncus wider at middle than at apex _____ 20
    Uncus widest at apex, strap-like _____ *A. jenia* n. sp.

20. Costal margin of sacculus with lobe at middle; ventral margin of valve forming a right angle at middle; apical part of valve nearly straight _____ *A. otasa* n. sp.
    Costal margin of sacculus not lobed; ventral margin of valve obtusely angled near middle; apical part of valve distinctly curved _____ 21

21. Lateral margins of uncus concave before apex _____ *A. kimsa* n. sp.
    Lateral margins of uncus straight or convex before apex _____ 22

22. Concavity of costal margin of valve as deep as width of valve at middle of concavity; sclerotized dorsal part of juxta v-shaped ____ *A. franclemonti* n. sp.
    Concavity of costal margin of valve not as deep as width of valve at middle of concavity; sclerotized dorsal part of juxta not v-shaped, dorsal edge sinuous and notched at middle _____ 23

23. Basal part of uncus with distinct, sharp pointed "shoulders" _____ *A. ivia* n. sp.
    Basal part of uncus without distinct, sharp pointed "shoulders" _____
    _____ *A. tusora* n. sp.

Aucula tricuspis Zerny
Figs. 1, 2, 49

Aucula (?) *tricuspis* Zerny, 1916: 188–189, pl. 5, fig. 4.
Aucula tricuspis, Draudt, 1919: 12.

Description. Length of forewing from base to apex: males, 18–23 mm, female, 22 mm. Maculation of upper and lower wing surfaces as in Figs. 1 and 2. Coloration of forewing a mixture of brick red and dark brown scales, lighter at costa and outer margin, darker at middle and inner margin. Forewing of *A. tricuspis* resembling that of *A. josioides* Walker and *A. munroei* n. sp., but with no tendency in *A. josioides* or *A. munroei* for costa and outer margin of forewing to be lighter than middle of forewing as in *A. tricuspis*; no lighter band toward apex of upper surface of forewing in *A. tricuspis* as in *A. josioides* and *A. munroei*. Pale area of hindwing smaller than in *A. josioides* and *A. munroei* (compare Figs. 1, 2, and 3). Outer third of costa on under surface of forewing black; in *A. josioides* and *A. munroei* outer third of costa dull yellow and adnate with yellow subterminal spot. Trilobed flattened process on front of head characteristic, distinguishing it from all other species of *Aucula* which have a conical frontal process. Male genitalia distinctive (Fig. 49), differing from *A. josioides* and *A. munroei* by presence of a hooked process at base of costa of valve and the absence of elongate hooked process arising from base of sacculus.

Type. A male, presumably in the Naturhistorischen Hofmuseums in Vienna from "Angabe des Fundortas, Brasilien."

Distribution. Known from the states of Minas Gerais, Goias, and the Federal District in east-central Brazil.

Discussion. We do not consider the extreme development of the frontal process to be of generic importance. Similar variation in the shapes of the frontal processes occurs in other agaristine genera and in some genera of other noctuid subfamilies.

FIGS. 1–8. *Aucula* spp. adults, dorsal and ventral views. **1–2.** *A. tricuspis* Zerny; **3–4.** *A. munroei* n. sp.; **5–6.** *A. josioides* Wlk.; **7–8.** *A. psejoa* n. sp.

Aucula munroei Todd and Poole, **new species**

Figs. 3, 4, 51

Description. Wing length from base to apex: males, 17–19 mm, female, 19 mm. Maculation of upper and under surfaces of wings as in Figs. 3 and 4, somewhat inter-

mediate between *A. josioides* and *A. tricuspis* in maculation and coloration, but most closely related to *A. josioides* in male genitalia (see Figs. 51 and 50) and presence of a conical frontal process. Yellow area of hindwing smaller, more restricted in *A. munroei* than in *A. josioides* (see Figs. 3 and 5); subterminal spot on upper side of forewing more distinct in *A. josioides* than in *A. munroei*. Conical frontal process larger than in *A. josioides*. Valve of male genitalia broader in *A. munroei* than in *A. josioides*, tegumen narrower and not ovate as in *A. josioides*.

Types. Holotype, male, Estacao Florestal, Cabeca do Veado, 1100 m, Districto Federal, Brazil, 20-X-1971, E. G., I., and E. A. Munroe, genitalia slide 37835 by E. L. Todd, in the Canadian National Collection; also 4 male and 1 female paratypes, same locality, from the 17th, 18th, 23rd, and 29th of October 1971, in the Canadian National Collection, and 2 males, same data, from the 16th and 31st of October 1971, in the United States National Museum.

Distribution. Known only from the type locality.

Discussion. This species has been named in honor of Eugene Munroe.

Aucula josioides Walker

Figs. 5, 6, 50

Aucula josioides Walker, 1862: 253; Hampson, 1910: 420; Strand, 1912: 52; Draudt, 1919: 12.

Description. Length of forewing from base to apex: males, 19–20 mm, females, 24–25 mm. Maculation of upper and lower surfaces as in Figs. 5 and 6. Male genitalia as in Fig. 50. Most closely related to *A. munroei*; distinguished from it as indicated in comments for that species.

Type. Presumably the type is a female in the British Museum of Natural History labeled "Petropolis, Rev. H. Clark." Walker stated that the specimen was a male collected by Fry from the vicinity of "Rio Janeiro." Hampson indicated that the only specimen in the British Museum at that time was the Petropolis specimen, but listed "Rio Janeiro" as additional data to the Petropolis label. This specimen is probably the type even though the sex disagrees with Walker's description and the specimen did not bear a type label in 1965 when it was examined. The lack of a type label is not surprising because Walker did not normally label his specimens as type and the specimen did not arrive at the British Museum until the museum acquired the Fry collection. We are sure Walker's name represents this species even if the Petropolis specimen is not the type because this species is so distinctive and has always been correctly identified in collections.

Distribution. Coastal mountains of the states of São Paulo and Rio de Janeiro.

Aucula psejoa Todd and Poole, **new species**

Figs. 7, 8, 52

Description. Length of forewing from base to apex: males, 23–24 mm. Maculation of upper and lower surfaces as in Figs. 7 and 8. A species characterized by its relatively large size; pale area of hindwing reaching inner margin as in *A. josioides*; forewings with transverse elements such as antemedial and postmedial lines still recognizable; a vague discal dot on underside of hindwing. Superficial appearance similar to remaining species of genus, except for remnants of transverse elements of forewings. Male genitalia distinctive, particularly in possessing large clavate cucullus (Fig. 52); uncus very reduced.

Types. Holotype, male, Incachaca, Cochabamba, Bolivia, J. Steinbach, genitalia slide J. G. F. 280, in the United States National Museum; 1 male paratype, Yungas del Palmar, 2000 m, Bolivia, leg. R. Zischka, genitalia slide RWP 38426 in the Zoologische Sammlung des Bayerischen Staates, Munich.

Distribution. The two known specimens are from the state of Cochabamba, Bolivia.

Discussion. *Aucula psejoa* appears to be intermediate in maculation and coloration between the preceding three species and those that follow. Though very distinctive, the greatly reduced uncus of the male genitalia indicates a relationship with *A. fona* new species.

Aucula hipia Todd and Poole, **new species**
Figs. 9, 10, 55, 76

Description. Length of forewing from base to apex: males, 20–21 mm. Maculation of upper and lower surfaces as in Figs. 9 and 10. Head, thorax, and abdomen reddish brown, abdomen darker than head and thorax. Palpi dark brown with white flecks. Upper surface of forewings dark reddish brown except outer third flecked with pearly white scales and subterminal yellow spot of under surface of wing showing through to a degree. Fringe of forewing dark reddish brown. Overall coloration of forewing in some lights slightly maroon. Hindwing with a black marginal band of approximately equal width all around margin of wing. Pale median area of hindwing approximately three times as long as wide, rounded at apex (Fig. 10). Prothoracic leg with reddish scaling on femur and tibia, dark brown on inner surfaces, flecked with white scales; tarsi dark brown flecked with white scales, ventral surface of tibia and femur with long white hairs. Mesothoracic leg dark brown with white flecks on tibia and tarsi, dorsal surface of tibia with long dull white hairs. Metathoracic leg dark brown with distal third and spurs of tibia white flecked; tarsi white flecked. Pectus of thorax with long dull white hairs. Tufts of yellow hairs at bases of forewing and hindwing. Hair pencil of base of abdomen pale yellow. Lower surface of wings dark brown except for yellowish areas. Yellow subterminal spot of forewing under surface not reaching costa, rounded at lower end, of approximately equal width throughout. Yellow median spot of hindwing under surface not reaching costa at base, produced into a tooth on subcostal vein approximately one-fourth to one-third distance to apex; inner margin of yellow spot straight, outer margin rounded. Male genitalia as in Fig. 55; recurved hook at base of costal margin of valve longer and thinner than in *A. gura* n. sp.; process of sacculus smaller and not as long or as well defined as in *A. gura*; large apical process of aedeagus glabrous and bifid (Fig. 76), not scobinate as in *A. gura* (Fig. 75).

Types. Holotype, male, Wineperu, Essequibo, Guyana, 29–31-III-69, Duckworth and Dietz, genitalia slide RWP 38427, in the United States National Museum; 1 male paratype, 39 mi. S.W. Wineperu, Mazaruni River, Essequibo, Guyana, 17–18-III-69, Duckworth and Dietz, in the United States National Museum; 1 male paratype, St. Jean de Maroni, French Guiana, received from LeMoult via Roths., genitalia slide 5159, in the British Museum of Natural History.

Distribution. Guyana and French Guiana.

Discussion. This species is remarkably similar to *A. gura* n. sp. from Peru, but differences in the male genitalia readily separate the two.

Aucula gura Todd and Poole, **new species**
Figs. 11, 12, 54, 75

Description. Length of forewing from base to apex: male, 22 mm. Maculation of upper and lower surfaces as in Figs. 11 and 12. Extremely similar to *A. hipia* n. sp. except subterminal spot of lower surface of forewing slightly narrower. Recurved hook on costa of valve of male genitalia (Fig. 54) shorter; triangular process from base of sacculus larger, longer, more sharply defined; aedeagus (Fig. 75) with sclerotized apex scobinate, not bifid.

Type. Holotype, male, Yahuarmayo, Peru, 1200', April–May 1912, genitalia slide ELT 5160, in the British Museum of Natural History.

Distribution. The unique specimen is from southeast Peru.

Discussion. *Aucula hipia* and *A. gura* seem to be closely related. These two species are also apparently related to *A. fona* n. sp., but probably not as closely as to each other.

FIGS. 9–16. *Aucula* spp. adults dorsal and ventral views. **9–10.** A. *hipia* n. sp.; **11–12.** A. *gura* n. sp.; **13–14.** A. *fona* n. sp.; **15–16.** A. *exiva* n. sp.

Aucula fona Todd and Poole, new species
Figs. 13, 14, 53

Description. Length of forewing from base to apex: male, 22 mm. Maculation of upper and lower surfaces of wings as in Figs. 13 and 14; distinguishable from all known

species of *Aucula* by a narrow, straplike, apically truncate, yellow spot on hindwing. Subterminal spot of under surface of forewing continued as a narrow yellow band around termen extending basad; in *A. gura* and *A. hipia* yellow does not reach termen. Male genitalia differing from those of *A. gura* and *A. hipia* by the very small spine at base of costa of valve; process at base of sacculus long and thin, not triangular; large triangular process at base of cucullus. Apex of aedeagus slender, not large as in *A. hipia* and *A. gura*, much more like aedeagi of other species.

Type. Holotype, male, Uberaba, Minas Gerais [Brazil], May–June 1924, bought from LeMoult, via Roths., genitalia slide ELT 4153, in the British Museum of Natural History.

Distribution. The state of Minas Gerais in Brazil.

Discussion. An easily identifiable species, probably most closely related to *A. hipia* and *A. gura*.

Aucula exiva Todd and Poole, **new species**
Figs. 15, 16, 56, 73

Description. Length of forewing from base to apex: males, 19–21 mm, females, 21–22 mm. Maculation of upper and lower surfaces of wings as in Figs. 15 and 16, superficially resembling *A. hipia*. Male genitalia (Fig. 56) distinctive, characterized by a large, spatulate process from near base of valve, process approximately two-fifths length of valve.

Types. Holotype, male, Pará [Brazil], A. M. Moss, via Roths., genitalia slide ELT 5180, in the British Museum of Natural History; 6 male and 3 female paratypes with the same data, all in the British Museum of Natural History.

Distribution. Known only from the state of Pará in Brazil.

Discussion. The process near the base of the valve of the male genitalia seems to relate the species most closely to the three new species *A. sonura, A. fernandezi,* and *A. nakia,* but the apex of the valve is similar to that of *A. hipia* and *A. gura.*

Aucula sonura Todd and Poole, **new species**
Figs. 17, 18, 57

Description. Length of forewing from base to apex: male, 21 mm. Maculation of upper and lower surfaces as in Figs. 17 and 18, superficially indistinguishable from *A. hipia.* Male genitalia (Fig. 57) characteristic, but indicating a species group relationship with *A. nakia* n. sp. and *A. fernandezi* n. sp.; apex of valve rounded, distal portion of costa covered by a narrow row of black spines; costal margin sinuous at middle immediately basad of long, straight spined apex; a small but prominent process near base of valve covered with black weak spines concealing curved dorsal surface which is provided with a series of large teeth.

Type. Holotype, male, Nari River, Antioquia, Colombia, genitalia slide JGF 277 in the United States National Museum.

Distribution. Known only from the unique type from the state of Antioquia in Colombia.

Discussion. The known range of this species may be useful in distinguishing it from *A. nakia* and *A. fernandezi,* its two closest relatives.

Aucula nakia Todd and Poole, **new species**
Figs. 19, 20, 58

Description. Length of forewing from base to apex: male, 22 mm. Maculation of upper and lower surfaces as in Figs. 19 and 20, superficially similar to *A. hipia*. Male genitalia (Fig. 58) similar to *A. sonura* but valve broader; black spines on apex of costa of valve terminating in a short projection basad; process from base of valve curved, lacking the tooth-like projections of *A. sonura*.

Type. Holotype, male, Callao, Peru, Coll. Mrs. M. J. Pusey, genitalia slide ELT

FIGS. 17–24. *Aucula* spp. adults dorsal and ventral views. **17–18.** *A. sonura* n. sp.; **19–20.** *A. nakia* n. sp.; **21–22.** *A. fernandezi* n. sp.; **23–24.** *A. buprasium* (Druce).

2125, in the United States National Museum; 1 male paratype, Rio Songo, Bolivia, 750 m, Fassl, in the British Museum of Natural History.

Distribution. The type is from the state of Lima on the coast of Peru. There is also a single male from Bolivia.

Discussion. The type locality of this species is an arid habitat in contrast to the apparently mesic localities of other members of the genus or of the paratype from

Bolivia. The genitalia obviously relate this species to *A. sonura* and *A. fernandezi*; the shape of the basal process of the valve is intermediate between these two species.

Aucula fernandezi Todd and Poole, **new species**
Figs. 21, 22, 59

Description. Length of forewing from base to apex: males, 18–19 mm. Maculation of upper and lower surfaces as in Figs. 21 and 22, similar to *A. hipia,* however, apex of under side of forewing beyond yellow subterminal spot distinctly lighter brown than remainder of wing. Male genitalia (Fig. 59) distinctive; black costal spines primarily limited to a small apical patch; middle of costal margin swollen; process from base of valve densely covered with spines but dorsal margin straight, not curved as in *A. sonura* and *A. nakia*; stout elongate spines present on tegumen.

Type. Holotype, male, Jusepin, Monagas, Venezuela, 28 October 1965, F. Fernandez Yepez and C. J. Rosales, genitalia slide ELT 3896, in the United States National Museum; 1 male paratype, St. Jean du Maroni, Guyana Francaise, in the United States National Museum; 3 male paratypes from the type locality, same data, 28-X-1965, 2-X-1965, and 10-IX-1965, in the collection of the Universidad Centrale de Venezuela, Maracay; 1 male paratype, Aroewara Creek, Maroewym Valley, Surinam, July 1905, S. M. Klages, in the British Museum of Natural History.

Distribution. So far known from eastern Venezuela, French Guiana, and Surinam. This species is probably found throughout the Guyana region.

Discussion. This species is related to *A. sonura* and *A. nakia,* but its known geographical distribution is disjunct from these two species. This species is named after Francisco Fernandez Yepez of the Universidad Centrale de Venezuela, who has greatly assisted with this and many other studies.

Aucula buprasium (Druce)
Figs. 23, 24, 60, 74

Leiosoma buprasium Druce, 1897: 300.
Aucula buprasia, Hampson, 1910: 420; Draudt, 1919: 12; Kiriakoff, 1977: 19.
Aucula buprasium, Strand, 1912: 51.

Description. Length of forewing from base to apex: male, 19 mm. Maculation of upper and lower surfaces as in Figs. 23 and 24, essentially similar to *A. hipia.* Male genitalia (Fig. 60) distinctive, valve terminating in a sharp point at apex without processes except basal projection of costal margin; basal projection covered with black spines; uncus greatly reduced, nearly obsolescent, membranous at base; tegumen swollen, moderately heavily sclerotized, ovate.

Type. Described from a single male from Sarayacu, Ecuador, genitalia slide ELT 5148, in the British Museum of Natural History.

Distribution. Known only from the unique type from central Ecuador.

Discussion. The illustration in Seitz is extremely poor or was based on another species which may have been standing in some collection under the name *buprasium.* The specific name is a city in Ancient Greece, hence the ending.

Aucula byla Todd and Poole, **new species**

Description. Length of forewing from base to apex: males, 19–23 mm, females, 23 mm. Maculation of upper and lower surfaces as in Figs. 25 and 26, similar to *A. hipia;* subterminal spot on under side of forewing somewhat variable, more rectangular than in *A. hipia* in specimens from northern Venezuela. Male genitalia (Fig. 61) of this species and following three exhibit some group characters, notably a moderately well-developed uncus; apex of uncus slightly enlarged, weakly bifid; costal margin of valve completely covered with spines, not in basal and apical patches as in other three species; a small knob-like process arising from the sacculus near base of valve.

FIGS. 25–32. *Aucula* spp. adults dorsal and ventral views. **25–26.** *A. byla* n. sp.;
27–28. *A. usara* n. sp.; **29–30.** *A. azecsa* n. sp.; **31–32.** *A. dita* n. sp.

Types. Holotype, male, El Limon, Aragua, Venezuela, 450 m, 3-X-61, F. Fernandez
Yepez, genitalia slide ELT 3893, in the United States National Museum; 1 male para-
type from the type locality, 14-VIII-60, and 1 male paratype from Rancho Grande,
Aragua, Venezuela, 1100 m, 20-VII-55, both in the collection of the Universidad Cen-
trale de Venezuela, Maracay; 1 male paratype, Rio Songo, Bolivia, 750 m, in the United

States National Museum; 2 male paratypes, Tinguri, Carabaya, Peru, 3400', dry season, August 04, G. Ockenden; 1 female paratype, same locality, wet season, Jan. 05; 4 male paratypes, La Oroya, R. Inambari, Peru, Sept. 04, 3100', dry season, G. Ockenden; 1 male paratype, Oconeque, Carabaya, Peru, 7000', dry season, July 04, G. Ockenden; 1 male, Rio Hacha, up to 9000', III, 98, Brown; 1 male paratype, Villavicencio, Colombia, 400 m, Fassl; 4 male paratypes, Rio Songo, Bolivia, 750 m, Fassl, all in the British Museum of Natural History.

Distribution. This species apparently ranges throughout the Andes and the northern mountains of Venezuela.

Discussion. At present this species seems to be the most widely distributed species of *Aucula*. It appears to be most closely related to *A. usara* n. sp. from the Amazon basin.

Aucula usara Todd and Poole, **new species**
Figs. 27, 28, 63

Description. Length of forewing from base to apex: male, 17 mm. Maculation of upper and lower surfaces as in Figs. 27 and 28, resembling *A. hipia* but distinctly smaller. Male genitalia (Fig. 63) with valve as in *A. byla* but with spines of costal margin of valve limited to base and apex; valves shorter than in *A. byla*.

Type. Holotype, male, Santarem, Amazones [Brazil], Fassl, genitalia slide ELT 2129, in the United States National Museum.

Distribution. The unique type is from the state of Amazonas in Brazil.

Discussion. *Aucula usara* is one of the smallest species in the genus. It is most closely related to *A. byla* and *A. azecsa* n. sp.

Aucula azecsa Todd and Poole, **new species**
Figs. 29, 30, 64

Description. Length of forewing from base to apex: males, 19–21 mm. Maculation of upper and lower surfaces as in Figs. 29 and 30, resembling *A. hipia* but smaller; slightly larger than *A. usara*. Male genitalia (Fig. 64) similar to *A. usara* but valve shorter, not produced at apex; apex of uncus slightly broader than in *A. usara*.

Types. Holotype, male, St. Jean Maroni, French Guiana, genitalia slide ELT 2130, and 1 male paratype, Geldersland, Surinam River [Surinam], in the United States National Museum; three male paratypes, St. Jean du Maroni, French Guiana, E. le Moult via Roths.; 1 male paratype, St. Jean Maroni, French Guiana, 1 male paratype, Bartica, British Guiana, 15-V-01, all in the British Museum of Natural History.

Distribution. Known from Guyana, French Guiana, and Surinam.

Discussion. The size and male genitalia of *A. azecsa* will separate it from other species occurring in the same area.

Aucula dita Todd and Poole, **new species**
Figs. 31, 32, 62

Description. Length of forewing from base to apex: males, 18–22 mm. Maculation of upper and lower surfaces as in Figs. 31 and 32, similar to *A. hipia*, but apex of upper surface of forewing lacking white scales of *hipia*; lower surface of forewing and hindwing black, not dark brown; size slightly smaller than *A. hipia*. Male genitalia (Fig. 62) with basal portion of costal margin of valve expanded dorsally into a large lobe, unlike three previously treated species; costal margin arcuate, an apical and basal patch of black spines present; process from base of sacculus larger than in previous three species.

Types. Holotype, male, Barro Colorado Island, Panama, 10–17-V-64, W.D. and S.S. Duckworth, genitalia ELT 2134, and 2 male paratypes, same data, in the United States National Museum; 1 male paratype, Lino, Panama, 800 m, Fassl, and 1 male paratype, Zaruma, Ecuador, 1891, M. de Mathan, both in the British Museum of Natural History.
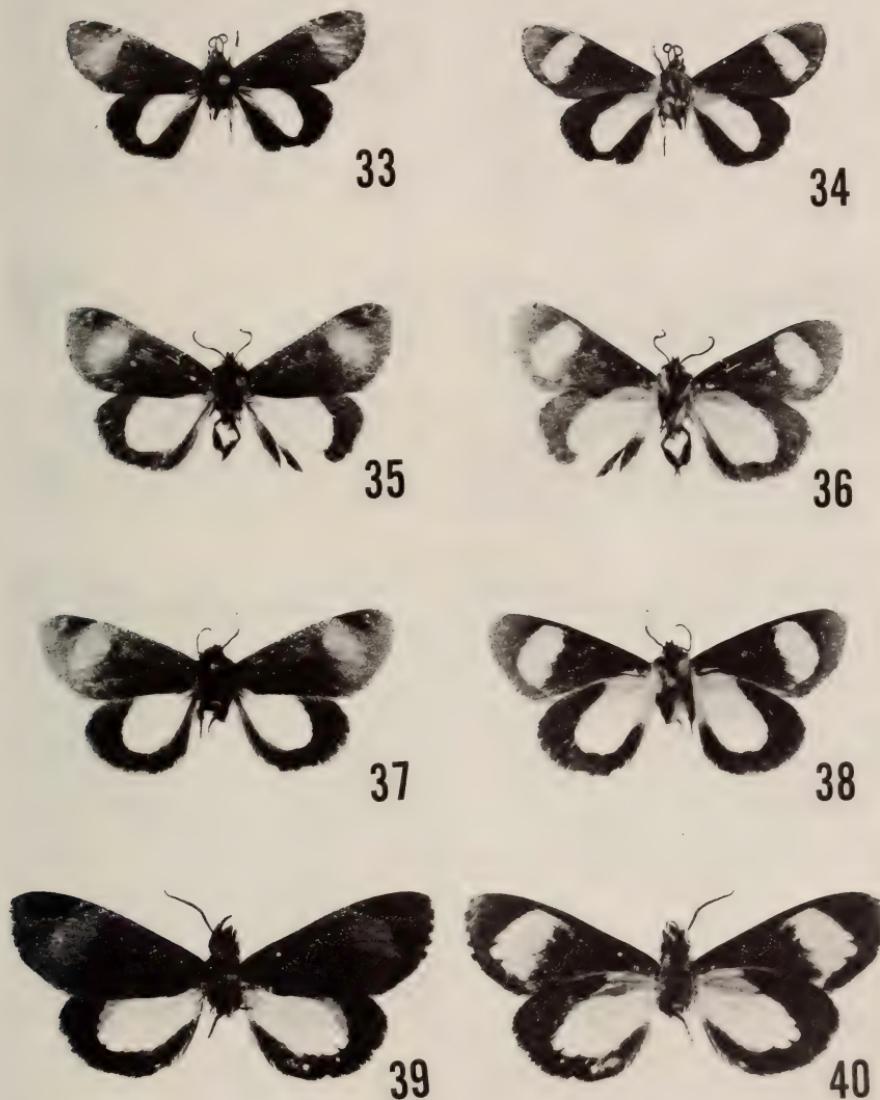
FIGS. 33–40. *Aucula* spp. adults dorsal and ventral views. **33–34.** *A. ceva* n. sp.; **35–36.** *A. tusora* n. sp.; **37–38.** *A. ivia* n. sp.; **39–40.** *A. franclemonti* n. sp.

Distribution. Known only from Ecuador and Panama.

Discussion. This species is the only one known to occur in Panama. In addition to the type series there are two females, one from Amazonas, Brazil and one from Ecuador that probably belong to this species. However, since females are difficult to associate with males, they have not been included in the type series.

FIGS. 41–48. *Aucula* spp. adults dorsal and ventral views. **41–42.** *A. otasa* n. sp.; **43–44.** *A. kimsa* n. sp.; **45–46.** *A. jenia* n. sp.; **47–48.** *A. lolua* n. sp.

Aucula ceva Todd and Poole, **new species**

Description. Length of forewing from base to apex: males, 16–20 mm. Maculation of upper and lower surfaces as in Figs. 33 and 34, similar to *A. hipia*, although perhaps a bit smaller. Male genitalia (Fig. 65) distinctive, apex of valve truncate; costal margin
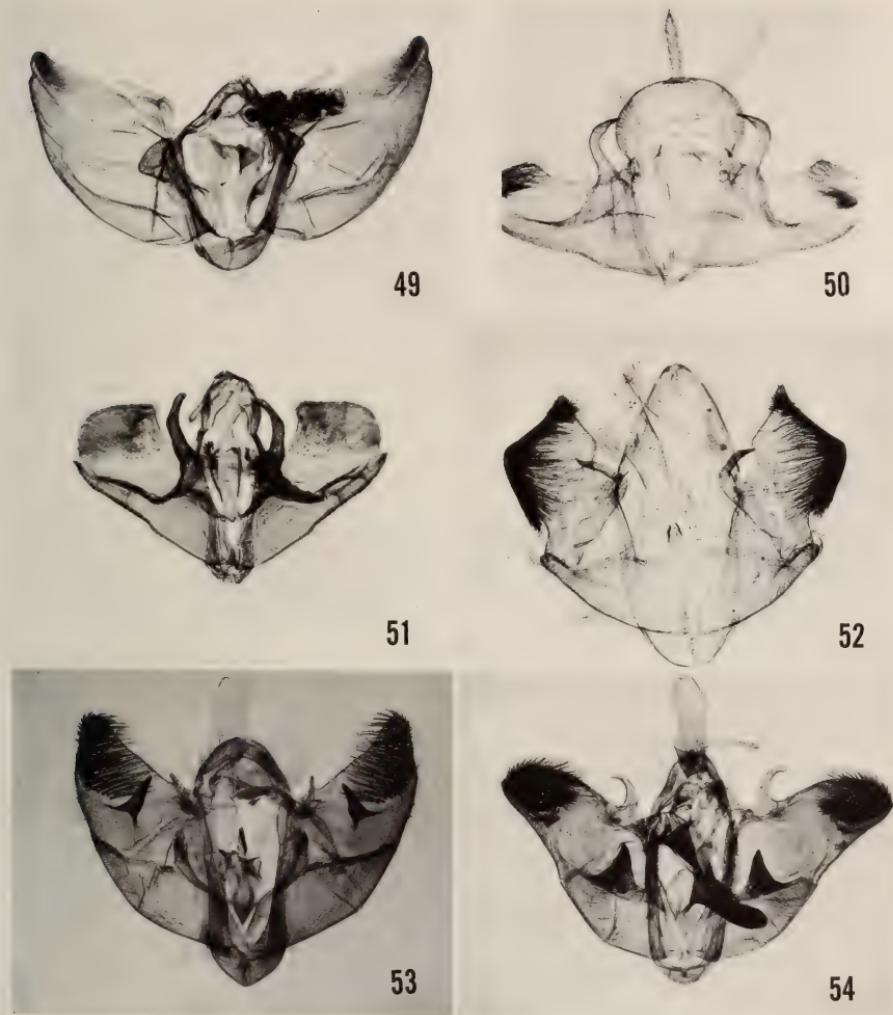
FIGS. 49–54. *Aucula* spp. male genitalia. **49.** *A. tricuspis* Zerny; **50.** *A. josioides* Wlk.; **51.** *A. munroei* n. sp.; **52.** *A. psejoa* n. sp.; **53.** *A. fona* n. sp.; **54.** *A. gura* n. sp.

of valve very short, less than half the length of ventral margin; apex of costa with a large cluster of black spines; base of costa with triangular process; dorsal margin of sacculus with two processes, one near base, other at basal third; uncus as in preceding four species but not enlarged at tip.

Type. Holotype, male, 60 miles up Maroni River [French Guiana], genitalia slide JGF 273, in the United States National Museum.

Distribution. French Guiana and probably Guyana and eastern Venezuela.

Discussion. Four male specimens in the British Museum of Natural History from St. Jean du Maroni, French Guiana and New River, British Guiana, and one male from Carrat el Dorado, Bolivar, Venezuela in the collection of the Universidad Centrale de Venezuela, Maracay are probably this species. The apex of the valve of the male gen-

italia of the French Guiana and Guyana specimens, however, is slightly concave and the ventro-apical angle is acute, not truncate as in the holotype. The transverse apical margin of the valve in the specimen from Venezuela is truncate but is toothed, not smooth. These specimens are not included in the type series because of these differences. Clearly more material will be needed to determine the significance of these genitalia differences.

Aucula tusora Todd and Poole, **new species**
Figs. 35, 36, 66

Description. Length of forewing from base to apex: male, 21 mm. Maculation of upper and lower surfaces as in Figs. 35 and 36. Valve reduced in width at apical one-third to two-fifths; ventral margin of valve angled at end of sacculus. Yellow spot of hindwing ovate to rounded, about twice as long as wide in this group of species. Genitalia of *A. tusora* with apex of uncus broad, somewhat diamond-shaped, basal portion tapering distally, not shouldered; reduced apex of valve rather stout, weakly curved; angle of ventral margin of valve obtuse; medial dorsal sclerotization of juxta lip-shaped.

Type. Holotype, male, "Bolivia," genitalia slide ELT 2126, in the United States National Museum.

Distribution. Known only from the holotype from some unknown locality in Bolivia.

Discussion. This species and the following five form a close group of species characterized by an enlarged broad uncus and a characteristically shaped valve. *Aucula tusora*, on the basis of the shape of the uncus, is most closely related to *A. franclemonti* n. sp., but the latter species has a more slender and curved apical part of the valve of the male genitalia. The sclerotized portion of the juxta is distinctly v-shaped in *A. franclemonti* but lip-shaped in *A. tusora*. The large ovate spot of the hindwing relates this species to the next five and to some degree to *A. josioides*.

Aucula ivia Todd and Poole, **new species**
Figs. 37, 38, 67

Description. Length of forewing from base to apex: males, 19–22 mm, females, 23 mm. Maculation of upper and lower surfaces as in Figs. 37 and 38, similar to *A. hipia* except for large, ovate, yellow spot on hindwing. Male genitalia (Fig. 67) are similar to those of *A. tusora* but uncus shouldered at base.

Types. Holotype, male, Incachaca, Cochabamba, Bolivia, J. Steinbach, genitalia slide JGF 279, and two male paratypes from the same locality, in the United States National Museum; 10 male paratypes, same data, in the Carnegie Museum; 1 male paratype, S. Domingo, Carabaya, Peru, 6000′, III, 02, wet season, Ockenden; 1 male paratype, S. Domingo, Carabaya, Peru, 6000′, Feb. 02, wet season, Ockenden; 1 male paratype, La Oroya, R. Inambari, Peru, Sept. 1904, 3100′, dry season, G. Ockenden; 1 male paratype, La Oroya, Carabaya, Peru, 3100′, IX, 05, G. R. Ockenden; 1 male paratype, Tinguri, Carabaya, Peru, 3400′, dry season, Aug. 1904, G. Ockenden, all in the British Museum of Natural History.

Distribution. Peru and Bolivia.

Discussion. Three female specimens, one from Peru and two from Bolivia, are probably this species, but since females have not been treated in this revision they have not been included in the type series. This species is apparently most closely related to *A. tusora* and *A. franclemonti*.

Aucula franclemonti Todd and Poole, **new species**
Figs. 39, 40, 68

Description. Length of forewing from base to apex: male, 27 mm. Maculation of upper and lower surfaces as in Figs. 39 and 40, similar to *A. hipia* except larger, lower half of outer margin of forewing more oblique to terman; yellow patch of hindwing
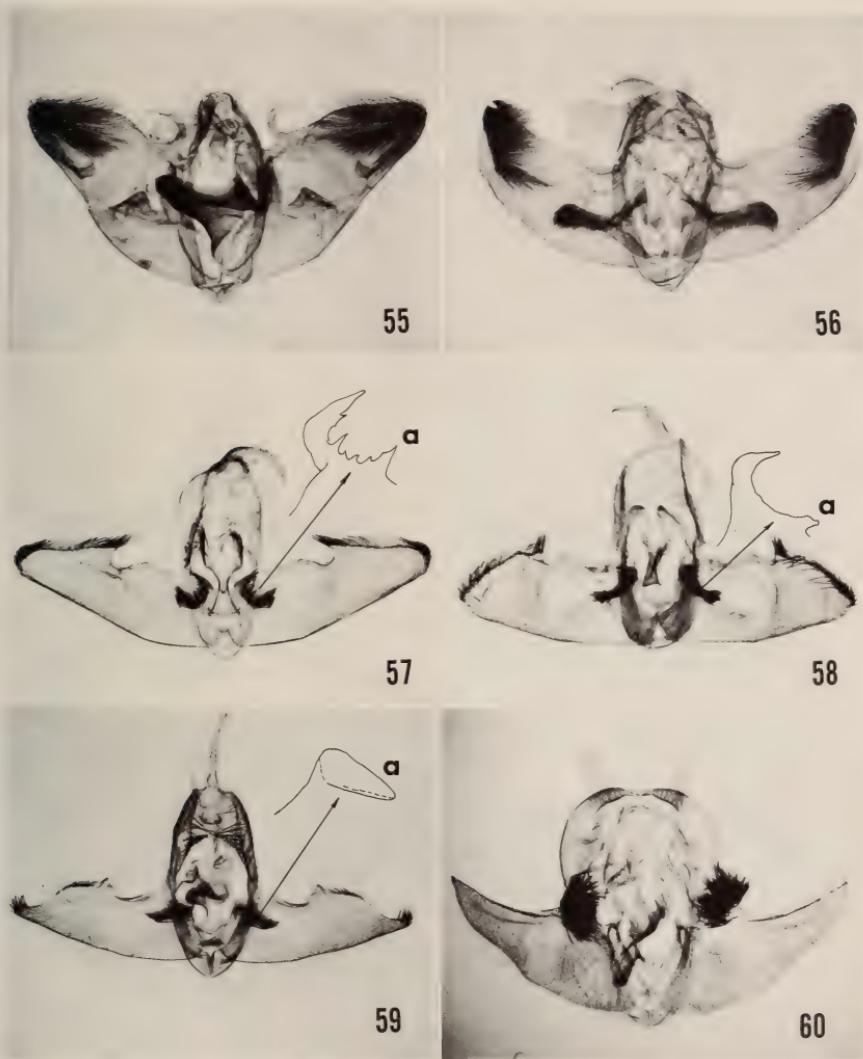
FIGS. 55–60. *Aucula* spp. male genitalia. **55.** *A. hipia* n. sp.; **56.** *A. exiva* n. sp.; **57.** *A. sonura* n. sp.; **57a.** *A. sonura* n. sp. detail; **58.** *A. nakia* n. sp.; **58a.** *A. nakia* n. sp. detail; **59.** *A. fernandezi* n. sp.; **59a.** *A. fernandezi* n. sp. detail; **60.** *A. buprasium* (Druce).

reaching inner margin at base. Male genitalia (Fig. 68) similar to *A. tusora* except apices of valves more slender and curved; uncus slightly smaller, but similar in shape, base without shoulders; sclerotization of juxta characteristically v-shaped.

Type. Holotype, male, San Antonio, Cali, Colombia, Fassl, genitalia slide JGF 272, in the United States National Museum.

Distribution. Known only from the unique type from Colombia.

Discussion. The shape of the uncus indicates a close relationship to *A. tusora* but
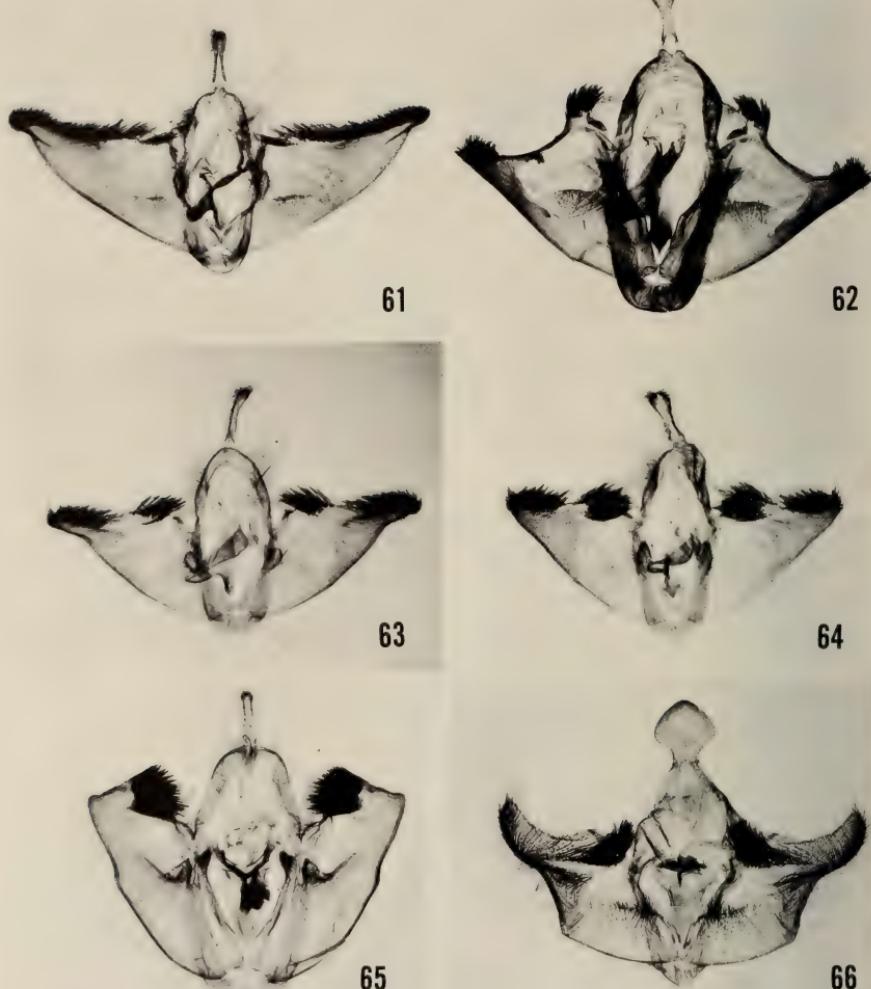
FIGS. 61–66. *Aucula* spp. male genitalia. **61.** *A. byla* n. sp.; **62.** *A. dita* n. sp.; **63.** *A. usara* n. sp.; **64.** *A. azecsa* n. sp.; **65.** *A. ceva* n. sp.; **66.** *A. tusora* n. sp.

on most other characters of the genitalia it is rather distinctive. In fact, *A. tusora* seems to be as closely related, if not more so, to *A. ivia*. This species is named in honor of John G. Franclemont, who initiated the study of this genus.

Aucula otasa Todd and Poole, **new species**
Figs. 41, 42, 69

Description. Length of forewing from base to apex: male, 17 mm. Maculation of upper and lower surfaces as in Figs. 41 and 42, similar to *A. hipia* except yellow spot of hindwing wider, more ovate, yellow reaching inner margin near base. Male genitalia (Fig. 69) distinctive; apex of valve nearly straight; angle of ventral margin very weakly
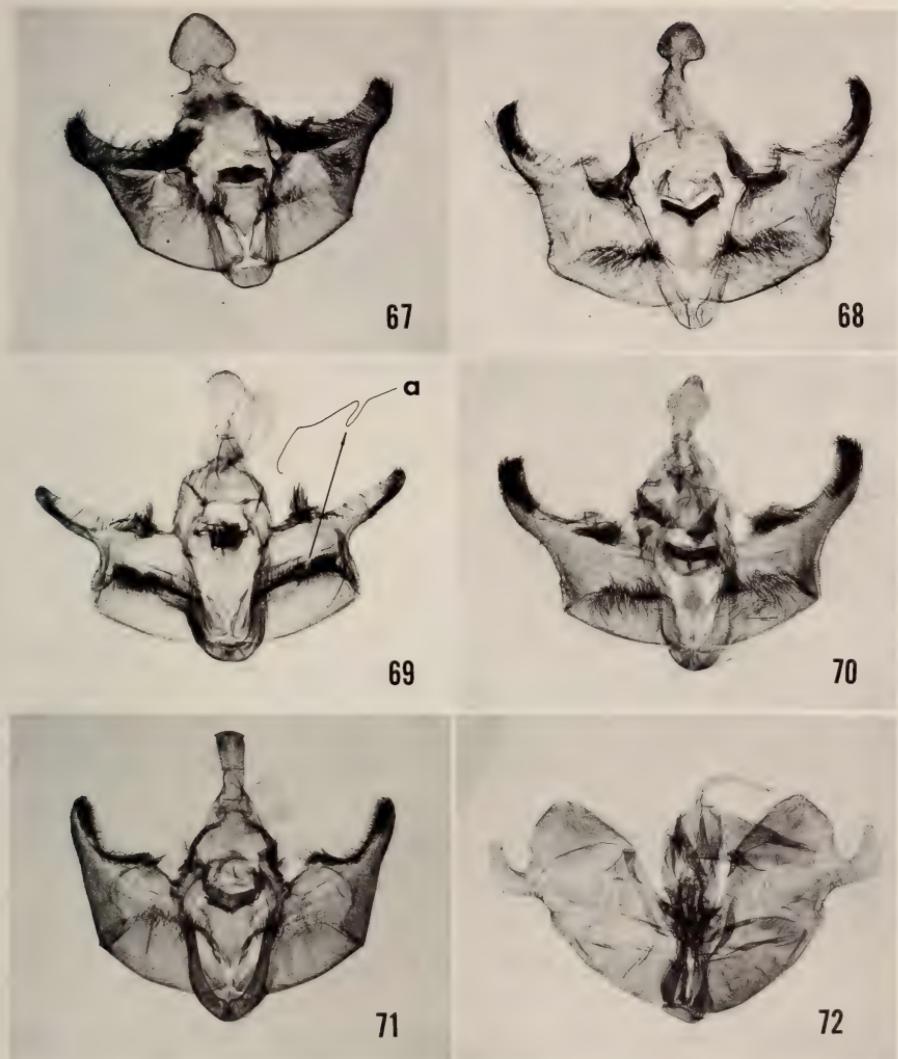
FIGS. 67–72. *Aucula* spp. male genitalia. **67.** *A. ivia* n. sp.; **68.** *A. franclemonti* n. sp.; **69.** *A. otasa* n. sp.; **69a.** *A. otasa* detail; **70.** *A. kimsa* n. sp.; **71.** *A. jenia* n. sp.; **72.** *A. lolua* n. sp.

obtuse, nearly right-angled; uncus strongly rounded at apex, spoon-shaped; dorsal margin of sacculus covered with a dense mass of setae, concealing a long outwardly oblique invagination, forming an elongate triangular lobe as illustrated.

Type. Holotype, male, Rio Sango, Bolivia, 750 m, Fassl, genitalia slide ELT 5219, in the British Museum of Natural History.

Distribution. Known only from the type locality in Bolivia.

Discussion. This is the third species of this species group from Bolivia. The straight apical part of the valve of the male genitalia probably indicates a close relationship to *A. jenia* n. sp.

FIGS. 73–76. *Aucula* spp. aedeagi. **73.** *A. exiva* n. sp.; **74.** *A. buprasium* (Druce); **75.** *A. gura* n. sp.; **76.** *A. hipia* n. sp.

Aucula kimsa Todd and Poole, **new species**
Figs. 43, 44, 70

Description. Length of forewing from base to apex: males, 26 mm. Maculation of upper and lower surfaces as in Figs. 43 and 44, resembling *A. hipia* except for larger, more ovate yellow spot of hindwing. Male genitalia (Fig. 70) similar to those of *A. franclemonti* except apical expansion of uncus with lateral edges broadly rounded; apices of valve slightly stouter and ventral margin near end of sacculus more sharply angled than in *A. franclemonti*; sclerotization of dorsal edge of juxta not as distinctly v-shaped as in *A. franclemonti*.

Types. Holotype, male, San Antonio, W. Colombia, Dec. 07, 5800′, M. G. Palmer, genitalia slide ELT 5167, in the British Museum of Natural History; 1 male paratype from the same locality also in the British Museum of Natural History.

Distribution. Known only from the type locality in Colombia.

Discussion. This species is closest to *A. franclemonti*, *A. ivia*, and *A. tusora*.

Aucula jenia Todd and Poole, **new species**
Figs. 45, 46, 71

Description. Length of forewing from base to apex: males, 23–24 mm. Maculation of upper and lower surfaces as in Figs. 45 and 46, similar to *A. hipia* except yellow spot of hindwing larger and more ovate and black discal dot present; lower surface of hindwing with black scaling on two veins of discal cell extending from discal dot to base of wing. Male genitalia (Fig. 71) vaguely similar to preceding five species, but with an apically truncate, strap-like uncus; narrow apical part of valve similar to *A. otasa*, slightly stouter; ventral margin of valve nearly straight, only weakly concave.

Types. Holotype, male, Paramba, [Ecuador], 3500′, Rosenberg, genitalia slide ELT 5152, in the British Museum of Natural History; 1 male paratype, Hacienda Cayandeled, Prov. Rio Bamba, Versant Quest Cordilleris, [Ecuador], 4200′, Feb. 1883, Stolzmann; 1 male paratype, Chimbo, Ecuador, 1897, M. de Mathan, both in the British Museum of Natural History.

Distribution. Known only from Ecuador.

Discussion. The black discal dot and markings on the under surface of the hindwing will separate this species from all other Andean species of *Aucula*.

Aucula lolua Todd and Poole, **new species**
Figs. 47, 48, 72

Description. Length of forewing from base to apex: male, 17 mm. Maculation of upper and lower surfaces as in Figs. 47 and 48, similar to *A. hipia* in maculation and coloration but smaller. Male genitalia (Fig. 72) distinctive valves very light sclerotized; basal two-thirds of costal margin of valves greatly expanded dorsally, slightly inclined toward apex; a convoluted, pointed process arising from just above middle of valve.

Type. Holotype, male, St. Jean de Maroni, French Guiana, Recd. from E. LeMoult via Roths., genitalia slide ELT 5170, in the British Museum of Natural History.

Distribution. Known only from the type locality.

Discussion. The genitalia of this species are uniquely different from all other species in the genus.

LITERATURE CITED

DRAUDT, M. 1919. *In* Seitz, A., Die Gross-Schmetterlinge der Erde, 7: 3–13, pl. 1.

DRUCE, H. 1897. Descriptions of some new species of Heterocera from tropical America. Ann. Mag. Nat. Hist. (ser. 6) 20: 299–305.

HAMPSON, G. F. 1910. Catalogue of the Lepidoptera Phalaenae in the British Museum, vol. 9. 552 pp., 10 pls.

JORGENSEN, P. 1935. Lepidopterous nuevos o raros de la Argentina y del Paraguay. An. Mus. Argent. Cienc. nat. 38: 85–130, 4 pls.

KIRIAKOFF, S. G. 1977. Lepidoptera Noctuiformes, Agaristidae. III. (American Genera). Das Tierreich, vol. 99. Walter de Gruyter. Berlin. 82 pp.

STRAND, E. 1912. Lepidopterorum Catalogus, part 5, Noctuidae, Agaristinae. Junk, Berlin. 82 pp.

WALKER, F. 1862. Characters of undescribed Lepidoptera in the collection of A. Fry, Esq. Trans. Ent. Soc. London (3)1: 253–262.

ZERNY, H. 1916. Neue Heteroceren aus der Sammlung des k.k. naturhistorischen Hofmuseums in Wien. Ann. des k.k. Naturhistorischen Hofmuseums 30: 173–195, 1 pl.

THE IMPORTANCE OF FOREST COVER FOR THE SURVIVAL OF OVERWINTERING MONARCH BUTTERFLIES (*DANAUS PLEXIPPUS*, DANAIDAE)

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ABSTRACT. When knocked to the ground or forced to land short of their roosts, monarch butterflies, too cold to fly, gain elevation by crawling up nearby vegetation. Although many occasionally fail to gain their roosts when returning from daily activities, they seldom remain overnight in forest clearings. Their behavior is explained by night ground temperatures being colder than those above the ground and by night temperatures under the forest canopy being warmer than those in forest clearings. If forced to remain on the ground in open areas for as little as one night, the majority suffer flight impairment or death. The meteorological conditions causing these climatic differences and the possible agent of impairment and death are discussed.

Millions of monarch butterflies spend the winter months in Mexico clustered on branches and trunks of trees. On warm days many thousands fly out of the colonies, principally to water. Depending on climatic conditions, varying numbers of healthy butterflies are found on the ground or on low foliage beneath the clusters. A few of those found on the ground are dead and yet show no obvious causes of death (Calvert et al., 1979).

Several environmental conditions can prevent butterflies from returning to roosting clusters. Falling temperatures, due to increasing cloud cover or onset of evening, effectively trap butterflies returning from daily activities when they land on the ground or low foliage. Direct physical actions of hail, rain, snow and wind also knock butterflies out of their roosts and occasionally cause butterfly-laden branches and tops of small trees to fall to the ground. After a storm butterflies continue to fall from water drenched roosts for several days (Calvert & Brower, ms. in prep.).

Once on the ground or low foliage, healthy butterflies, too cold to fly, shiver in an attempt to raise their thoracic muscles' temperature (Douglas, 1979; Kammer, 1971) to a point where they can fly back to a cluster or, if the temperature is too low for flight, attempt to crawl up any available foliage (Fig. 1). Some of these, however, due either to lack of appropriate foliage or to decreasing temperatures, are unable to get off the ground. These butterflies eventually close their wings and become dormant. Long periods of inclement weather may keep butterflies grounded for several days, because ambient thermal conditions do not reach the temperature required for flight.

These observations suggested that being forced to remain on the ground overnight or longer was potentially harmful to the butterflies

and prompted experiments using naturally occurring temperature and humidity regimes. We asked, first, if inclement conditions could result in butterfly mortality and, second, what advantages roosting in the forest might provide. By comparing climatic effects of forested and open areas on butterfly mortality, we also began to inquire into the effects of local forest management on these butterflies.

Materials and Methods

During January 1980 at a Mexican overwintering site of approximately 0.21 hectares located 2 km southeast of a previous colony designated Site Alpha (Brower et al., 1977), we exposed groups of butterflies to ambient conditions for several nights in two areas differing greatly in microclimate. In the evening when temperatures were approximately 10°C, too cold for butterflies to fly, we placed 90 butterflies obtained from a roost in the colony in three topless hardware-cloth enclosures (Fig. 2) as follows: fifteen butterflies of each sex were placed in each of two enclosures located in a 0.5- hectare deforested area (hereafter called "open area"); fifteen butterflies of each sex were also placed in an enclosure located within the colony approximately 100 m from the open area. All butterflies were in the same apparent physical condition. To keep the butterflies at ground level, we removed vertical vegetation from the enclosures and when necessary picked them off the walls.

The following day we allowed individual butterflies an opportunity to fly by tossing them into the air during a warm period when other butterflies were flying. If a butterfly flew irregularly or could not fly at all, we assigned it to one of two categories of disability: "flight impaired" or "moribund" (Table 1). Butterflies failing the initial flight test were given another opportunity to fly.

A second group of 90 butterflies was exposed for two nights before flight-testing. In addition, this group was weighed in subgroups of 15 by sex each evening and morning in order to monitor weight gained because of dew or frost (Table 2). They were also weighed each evening after all dew had evaporated to determine weight loss due to desiccation (Table 2). Those butterflies remaining after the flight-test in both groups of 90 were exposed for two additional nights, their weights recorded evening and morning, and then flight tested once again.

During the day, all butterfly groups were kept in wide mesh nylon cages shielded from direct sunlight. A Pesola 50-g balance accurate to 0.1 g was used to weigh the butterfly groups and a PSG max-min thermometer was used to monitor nightly minimum temperatures.

FIG. 1. Monarch butterflies knocked down from their roosts by a snowstorm. Some have managed to get into relatively warmer air by crawling up the stem of *Senecio angulifolius* DC. Original 35-mm Kodachrome by Willow Zuchowski.

FIG. 2. Hardware cloth enclosure used to delimit observation areas. Heavily frosted butterflies lie on the ground. Butterfly at top center (arrow) is more upright in posture and consequently did not suffer as much frosting. Inset: Enlargement of frosted butterflies in enclosure (2×). Original 35-mm Kodachrome by William Calvert.

RESULTS

Grounded butterflies exposed one or two nights in the open area experienced lower temperatures (3-night average = $-1.7°C$; range = -1.1 to $-2.2°C$) than the corresponding group within the colony (3-night average = $+1.9°C$; range = 2.8 to $1.1°C$; Table 1). Furthermore, the open area groups took on more dew and/or frost, gaining an average of 0.15 g or 22.5% of their weight in water, compared to only 0.003 g or 0.6% for the colony groups (Table 2). The groups in the open suffered an average of 60% more flight impairment and mortality than the control groups exposed within the colony (Table 1). Expected differences due to the time exposed are also evident. After one night in the open area 40% of the butterflies flew off normally, while only 30% did so after two nights (Table 1). In addition to the data given in Table 1, at the end of two additional nights of exposure all but one of the remaining butterflies were dead or moribund. In contrast, all butterflies exposed within the colony flew off normally, even after two nights of exposure (Table 1).

Weight loss due to desiccation was small, averaging only 0.001 g or 1.5% of their body weight (Table 2). Most of this loss occurred between the third and fourth evenings, suggesting that some of the ani-

Table 1. The effect of exposure of grounded butterflies to nighttime conditions on flight and survivorship.

| Position of enclosure | Expt.[1] no. | No. nights exposed | Percentage of butterflies at end of exposure | | | | Minimum nightly ground temperature T°C |
			Normal	Flight[2] impaired	Moribund[3]	Dead	
Experimentals:	1	1	47%	27%	23%	3%	−2.2
(On ground in open area adjacent to colony)	2	2	33%	47%	20%	0%	{ −1.7 −1.1
	3	1	33%	27%	37%	⸱3%	−2.2
	4	2	27%	10%	60%	3%	{ −1.7 −1.1
Controls:	5	1	100%	0%	0%	0%	1.1
(On ground under trees within colony)	6	2	100%	0%	0%	0%	{ 2.8 1.7

[1] Each experiment consisted of 15 ♀♀ and 15 ♂♂.
[2] Butterfly attempted to fly but landed within 10 m for 2 consecutive trials.
[3] Butterfly was alive but unable to fly.

mals may have died before the final weighings. Both the small magnitude of weight lost and the lack of difference between weight loss occurring in the colony and in the open area make weight loss an unlikely factor in the mortality of these butterflies. Since there was no net weight gain from evening to evening, it is clear that the water deposited as dew remained on the surface and was not absorbed by the animals.

Discussion

This study shows that butterflies experience flight impairment and increased mortality when grounded in an open area. Normally, how-

Table 2. Weight gains due to nightly accumulations of dew or frost and weight loss due to desiccation. Figures are the percentage of final weights which is water.*

Position of enclosure	Expt. no.	Number of butterfly days†	Percent weight gained from evening to morning	Percent weight lost from evening to evening
Experimentals:	2	101	22.1%	2.6%
(On ground in open area adjacent to colony)	4	98	22.8%	0.9%
Controls:				
(On ground under trees within colony)	6	51	0.6%	1.1%

$* = \dfrac{\Sigma \text{ weight gain or loss}}{\Sigma \text{ final weights}} \times 100.$

† = Σ Number butterflies exposed each night × number of nights.

ever, butterflies do not remain overnight in cleared areas. Two factors increase the likelihood of their exposure to conditions similar to or approaching those found in open areas. (1) Periods of cold inclement weather in Mexico's transvolcanic belt lasting up to six days have been witnessed by us and are evident in local weather records kept by the Mexican National Weather Service. (2) Local logging activities, even though they do not involve clear cutting, continue to produce open spots and thinned areas, thereby reducing the moderating effect of the natural forest on extremes of temperature and humidity.

Long term weather records (10–29 years) available from eight standard meteorological stations near the overwintering areas above 2500 m altitude show monthly extreme minimum temperatures for December, January and February averaging −5.2°C, −6.4°C and −6.4°C respectively (Anon., 1976). These stations are always located in open areas where minimum temperatures would be lower than those occurring in adjacent forested areas. If damping effects of the forest are on the order of those indicated in Table 1 ($\bar{x}$ = 3.5°C), temperatures as low as −2.5°C are expected near the ground within the colonies— a temperature sufficiently low to cause flight impairment, moribundity and death after only one night of exposure (Table 1). It should be noted that the average altitude of the butterfly colonies is ca. 3000 m, while the average for the eight nearby weather stations is only 2589 m. Even colder temperatures are therefore expected at the higher overwintering colony altitudes.

Within the overwintering areas, we have personally witnessed the destructive effects of local storms during the past four years. Of particular severity were storms lasting from 6–8 February 1978 and from 21–26 January 1980. The former dropped 7-mm diameter hail pellets on at least two colonies; the latter storm brought as much as 25 cm of snow to adjacent open areas. Tens of thousands of butterflies were knocked down from their clusters, pelted with hail, and frosted or covered with snow (Figs. 3 and 4).

Since butterflies stranded on the ground in open areas experience a very different microclimate from those on the ground in the colonies, a review of some important microclimatological parameters pertinent to these altitudes is in order (see Geiger, 1965 for a more complete discussion of microclimate). The differences are primarily due to a difference in location where nighttime cooling occurs. In both open and forested areas, cooling takes place at night from all plant and soil surfaces, but, for reasons discussed below, cooling is most effective at the interface between plant and open sky, i.e., near the ground in open areas and at canopy level in forested areas. Beneath and within plant canopies, radiational cooling of any object is in general diminished by a dynamic interchange of radiation

FIGS. 3 & 4. Butterflies knocked to ground by a snowstorm. Some are partially buried in the snow (arrows). Some have oriented upslope so they can bask whenever the sun appears. Others have crawled onto low-lying vegetation. Original 35-mm Kodachrome photos by William Calvert.

involving absorption and subsequent reradiation, mainly by adjacent plant parts, but also by other adjacent objects, water vapor and CO_2 (band radiation) and the reabsorption of radiation by the object. Above the vegetational layer, however, water vapor and CO_2 play only a minor role as an impediment to outgoing radiation. Not only is the absolute humidity low during the overwintering period (this period closely corresponds to the Mexican dry season), but also at night; at these altitudes all objects are near 0°C, a temperature for which the water vapor and CO_2 absorption coefficients are very low (Geiger, 1965). Little absorption and subsequent reradiation (back radiation) takes place at the top-most plant layer since no plant parts or other objects lie above it, and water vapor and CO_2 are inefficient absorbers at temperatures prevailing at night. Heat received and stored during the day by this layer is radiated almost unhindered at night.

The primary source of heat at night is that stored in the ground. Ground heat is transferred to nearby objects by longwave radiation and eddy diffusion. In addition, the butterflies receive some heat through band radiation of atmospheric water vapor and CO_2, but this is diminished for reasons discussed above. These objects lose heat by longwave radiation to the atmosphere and cosmic cold, and by convection and evaporation. Principally, because no heat is returned by conduction as occurs in the ground, these objects cool more rapidly than the ground itself. Consequently, dew deposition and frost are likely to occur on them first (Geiger, 1965).

Thus, a butterfly grounded in an open area loses heat to the atmosphere and cosmic cold by radiational and evaporative cooling, gains none back by conduction and only a little back by absorption and reabsorption of longwave radiation or by eddy diffusion of ground heat upward. Once night sets in, a butterfly cools more rapidly than the surrounding air, dew deposition begins, and then frost occurs. On the other hand, a butterfly positioned beneath the forest canopy is in near radiational equilibrium with plant parts and other butterflies. Most of the cooling action is occurring above it at the interface of canopy and sky. Water vapor pressure within the colony is generally higher, and convection less; consequently, evaporation is less and more longwave radiation is reabsorbed. These conditions greatly moderate the low temperatures occurring in nearby open areas.

Because of these microclimatic factors, crawling up onto vegetation (Fig. 1) is an appropriate response for butterflies stranded near the ground when air temperatures preclude flight. During windless nights, movement one meter upward would take them into air that is an average of 3.3°C warmer than air at ground level (Siegel *In* Geiger, 1950). Our measurements of minimum temperatures during a clear

night at Site Alpha indicated that the minimum temperature at 1-meter elevation was 2.5°C warmer than on the ground. Additional benefits of crawling onto vegetation may accrue due to increases in back radiation from overhead plant foliage and perhaps also to increased safety from small mammal predation. These aspects of this remarkable behavior are currently being investigated.

Temperature differences *per se* may not wholly account for differences in survival rates between exposed butterflies in open and forested areas. Using laboratory facilities, Urquhart (1960) subjected groups of monarchs to 12-hour low temperature regimes and found complete recovery in adults subjected to temperatures as low as −6.8°C. Since temperatures this low were never encountered by us at the Mexican overwintering sites, the incapacitation of 60% of butterflies exposed one night to a minimum temperature of −2.2°C (Table 1) suggests that frost may be more important than low temperatures *per se*.

In studies investigating the effect of moisture or ice in contact with the insect exoskeleton, Salt (1936) found that freezing moisture on the surface of an insect was effective in the initiation of freezing within by the growth or propagation of external ice into the body of the insect, a process he called inoculative freezing. No such enhancement of freezing was found, however, when ice was placed in contact with the dry surface of a cooled insect (Aoki & Shinozaki, 1953). Bevan & Carter (1980) also found moisture to be critical to mortality. Their results suggested, as do ours, that freezing of dew condensed on the insect's surface initiates internal freezing at temperatures higher than it would occur if the surface was dry. By crawling upward these butterflies escape both the higher humidities and lower temperatures found near the ground; and hence, they escape the dangers of having ice in contact with their exoskeletons.

Summary and Conclusion

Butterflies are often trapped on the ground for one or more nights, due to a variety of environmental circumstances. Ground conditions are in general colder and wetter than those prevailing above the ground. Sixty percent of butterflies exposed to ground conditions for one night in an open area suffered flight incapacitation or died. By crawling up off the ground to avoid the coldest and wettest areas, the butterflies remove themselves from the dangers of inoculative freezing.

In all but the most inclement weather, the moderating effect of the forest canopy protects the butterflies from temperature extremes; all butterflies exposed to these conditions, even though prevented from

crawling off the ground, survived. However, several times a year during storms or cold spells, ground temperatures beneath the forest canopy become cold enough to incapacitate or kill them. Under these circumstances crawling up into warmer temperature zones would probably enhance their survival.

When the forest is thinned, meteorological conditions are expected to approach those found in forest clearings; the moderating effect of the forest will be diminished; butterfly mortality is expected to rise. Because of the increasing pressures of forestry in these areas of Mexico, even though the practices lie within the bounds of good forest managment, it is urgent and essential to establish relationships between weather, forest thinning, and butterfly survival in the overwintering areas.

ACKNOWLEDGMENTS

LITERATURE CITED

ANONYMOUS. 1976. Normales Climatologicas. Direccion General de Geografia y Meteorologia. Servicio Meteorologico Nacional, Mexico D.F.

AOKI, K. & J. SHINOZAKI. 1953. Effect of cooling rate on the undercooling point of the prepupa of slug moth. Low Temp. Sci., 10: 109–115 (In Japanese with English summary).

BEVAN, D. & C. I. CARTER. 1980. Frost-proofed aphids. Antenna (Bull. Royal Entomol. Soc. London), 4(1): 6–8.

BROWER, L. P., W. H. CALVERT, L. E. HEDRICK & J. CHRISTIAN. 1977. Biological observations on an overwintering colony of monarch butterflies (Danaus plexippus, Danaidae) in Mexico. J. Lepid. Soc., 31: 232–242.

CALVERT, W. H., L. E. HEDRICK & L. P. BROWER. 1979. Mortality of the monarch butterfly (Danaus plexippus L.): Avian predation at five overwintering sites in Mexico. Science, 204: 847–851.

DOUGLAS, M. 1979. Warm-blooded butterflies have developed interesting warm-up techniques. Michigan Natural Resources, 48(3): 11–13.

GEIGER, R. 1965. The Climate Near the Ground. Harvard University Press, Cambridge, Massachusetts. 482 pp.

KAMMER, A. E. 1971. Influence of acclimation temperature on the shivering behavior of the butterfly, Danaus plexippus (L.). Z. Vergl. Physiol., 72: 364–369.

SALT, R. W. 1936. Studies on the freezing process in insects. Tech. Bull. Minn. Agric. Exp. Stn., 116, 41 pp.

SIEGEL, S. In Geiger, R. 1950. The Climate Near the Ground. Harvard University Press, Cambridge, Massachusetts, pp. 64–65.

URQUHART, F. A. 1960. The Monarch Butterfly. Univ. Toronto Press, Toronto, Canada. 361 pp.

REDISCOVERY OF *APODEMIA PHYCIODOIDES* (RIODINIDAE)

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ABSTRACT. *Apodemia phyciodoides* Barnes & Benjamin had previously been known only from the holotype and allotype, which were taken in the Chiricahua Mountains of Arizona. Evidence indicates that these were captured by O. C. Poling, possibly in 1915. During 1978, 1979 and 1980, the authors took about 50 specimens from four major drainages on both sides of the continental divide in the Mexican states of Chihuahua and Sonora. Specimens were recorded in the months of April, June, August and September.

Technical literature today abounds with anecdotes of 19th century naturalists, but we are discouraged from relating contemporary incidents in scholarly journals. This policy deprives posterity of what may someday be of considerable interest. (It would be highly amusing to know Paul Ehrlich's first words when handed the first specimen of what Clench and he later named *Sandia macfarlandi*.) Toward this end, we offer the following informal account of the rediscovery of *Apodemia phyciodoides*, a butterfly "lost" for more than 60 years.

A. phyciodoides was described by William Barnes & F. H. Benjamin (1924), based on a male holotype labelled "Chiricahua Mountains/Cochise Co./Ariz." and an allotype labelled "Paradise/Cochise Co./Ariz." These specimens are presently in the U.S. National Museum of Natural History collection.

While we cannot be sure who collected the type material, available evidence points strongly to O. C. Poling, a pioneer collector/dealer in the southwestern U.S. In a letter to Henry Skinner dated 20 August 1915, Poling indicated he had been collecting "since early spring" with two assistants at Paradise, Arizona, and intended to return to Quincy, Illinois, on "Oct. 1st." This letter was written on stationery with the letterhead of the "Paradise Mining and Milling Co." Poling was a supplier of specimens to a number of eastern lepidopterists, including Skinner and Barnes. His style of concentrated collecting for long periods at one locale (as in the Baboquivari Mountains, Arizona, and Davis Mountains, Texas) resulted in unusual records and series of specimens that have never been duplicated. We have a specimen of *Catocala delilah desdemona* Hy. Edwards with a locale label bear-

ing identical data (though set in different type) to that of the *phycio-doides* allotype. This specimen was obtained from A. E. Brower, who in turn related that Otto Poling had collected "a large number of *C. d. desdemona* in the Southwest."

In any event, no further specimens of *phyciodoides* were apparently taken until 1978, despite intensive searching in southeastern Arizona, especially in the last 20 years. Thus, the species has been rarest of all Nearctic butterflies in collections.

The senior author has been desirous of traversing the Sierra Madre Occidental in Mexico since 1964. In April 1978, a serious attempt finally became possible. While this attempt did not accomplish the primary objective, an unrecognized *Apodemia* was taken at a number of sites, initially near Colonia Juárez, Chihuahua. Interestingly, this site is very close to the type locality of *Speyeria nokomis coerulescens* Holland (1900), where Charles H. T. Townsend had collected in 1899 (see Fig. 1). Townsend took at least four other taxa which were undescribed at the time (Clench, 1965). It is surprising that neither Townsend nor subsequent *coerulescens'* collectors in the area found *phyciodoides*.

Coincidence entered the story in April 1979, when Holland decided to make 1979 the year to survey the Organ Mountains near Las Cruces, New Mexico (Holland, 1974). There conversations with the junior author, who was doing research on *Apodemia* at the New Mexico State University, turned to the unrecognized *Apodemia* from the Sierra Madre. On Holland's next trip to Las Cruces, he taped an envelope with unspread specimens to Forbes' door, went collecting in the Organ Mountains, and returned to Albuquerque, where an excited Forbes had been trying for some time to call him concerning the identity of the *Apodemia*.

A joint trip to Colonia Juárez in June of 1979 yielded additional *phyciodoides* specimens and new collection sites, and fulfilled Holland's ambition of 15 years to traverse the Sierra Madre. Forbes made additional trips in August and September of 1979, which provided further records of flight periods. Fig. 2 illustrates a typical specimen from that locality. We now believe *phyciodoides* is widely distributed throughout the northeastern extremity of the Sierra Madre and is multiple brooded from at least April to September. Our records follow in the Appendix. That the rarest Nearctic butterfly has been abundantly flying just 100 miles south of the border the last 60 years should serve to impress all collectors in the American Southwest of the lepidopterists' "rose garden" right in our backyard.

The ecological associations of *phyciodoides* are imperfectly known. At Colonia Juárez, it appeared to be most common at the mouth of
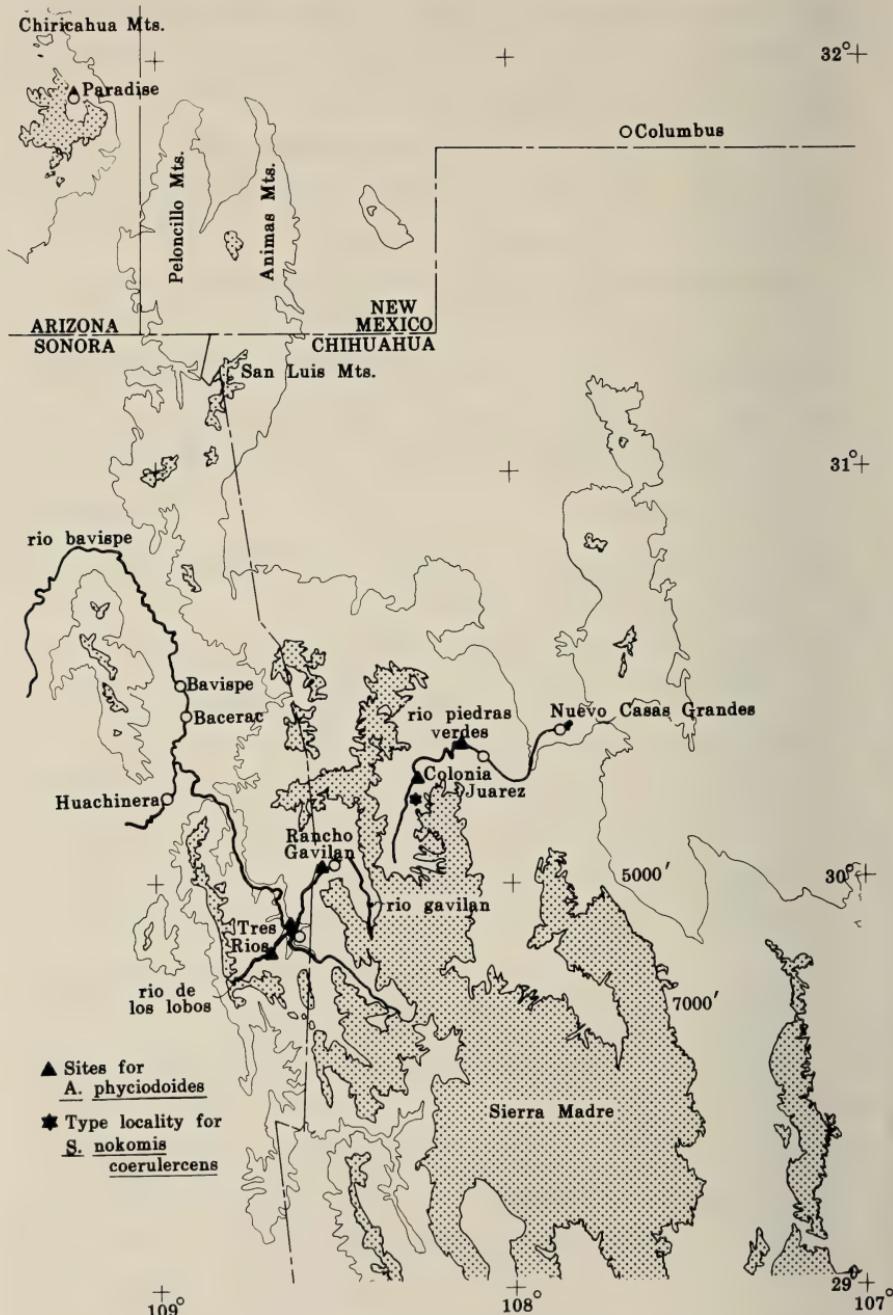
FIG. 1. Locations at which *Apodemia phyciodoides* has been found, with indication of 5000′ and 7000′ elevation contours.

narrow canyons opening on the Rio Piedras Verdes in a *Prosopsis-Celtis-Aloysia* association. Several specimens were taken at blooms of annual *Eriogonum*. A few individuals were collected in grassy clearings adjacent to the *Baccharis-Salix* vegetation along the stream, but the species does not appear to be riparian in the manner of *Calephelis* (it was never collected at profuse *Baccharis* blooms along the stream). It was also collected in adjacent grassy canyons among shrubs of *Quercus* and *Aloysia* but was not found in the xeric, mesquite-ocotillo, desert-scrub bordering the river canyon. One specimen was taken along with *Apodemia nais* (Edw.) on the Rio de Los Lobos (see Fig. 1) in the lower pine zone, indicating that the species extends to higher elevations; a broad altitudinal range is not unusual in *Apodemia*.

A peculiarity of Sierra Madre collections is the lack of records for *Apodemia palmeri* (Edw.), which is often abundant in *Prosopsis-Baccharis* habitat such as occurs at Colonia Juárez. The correlation between presence of *phyciodoides* and absence of *palmeri* is one that requires further study. To our knowledge, *Emesis zela cleis* (Edw.) is the only other riodinid thus far collected at Colonia Juárez, although *Calephelis nemesis* (Edw.), *C. arizonensis* McAlpine and *Apodemia hepburni* Godman & Salvin might also occur there (at the Tres Rios site, *phyciodoides* and *arizonensis* have been taken together). From our limited experience, *phyciodoides*, where present, would seem considerably less common than *A. palmeri*, but somewhat more abundant than *A. hepburni* (which itself is very poorly known).

In concluding, we must consider the apparent absence of *phyciodoides* from the Chiricahua Mountains today. There seems little reason to doubt the data on the type specimens. Until recently, the insect was not known from elsewhere, and if Poling was the collector, his locally intensive field work might have yielded an otherwise overlooked riodinid. Poling's locale labels, although often imprecise, are usually considered reliable.

We might then consider the possible recent extinction of *phyciodoides* in southeastern Arizona. There is at present no habitat on the eastern side of the Chiricahua Mountains that exactly matches the Colonia Juárez locality. The area around Paradise is higher (elevation 5800′) and is more heavily grown with oaks and junipers. Yet, at the same time it lacks the permanent riparian habitat characteristic of all known *phyciodoides* sites. We have no way of knowing if the types were captured at higher, wetter locales west of Paradise or at more xeric spots to the east.

There are presently stretches of open desert that effectively separate the Sierra Madre from the Chiricahua Mountains from the stand-

point of *phyciodoides* dispersal. Evidence exists for a drying trend in this region (Schulman, 1956) with resultant elevation of life zones. As stated by Lowe (1964), even a slight change in the precipitation-evaporation ratio can markedly change the vegetation at one locality. From Fig. 1 we may visualize a time when more of a vegetative continuum existed between the Sierra Madre and the Chiricahuas. It is thus fully possible that a declining relictual population of *phyciodoides* inhabited the Chiricahuas until early in this century and has been extinguished without a natural means of introduction. However, we must temper such speculation with the observation that only two specimens were captured in the first place and that its precise habitat requirements are still poorly known.
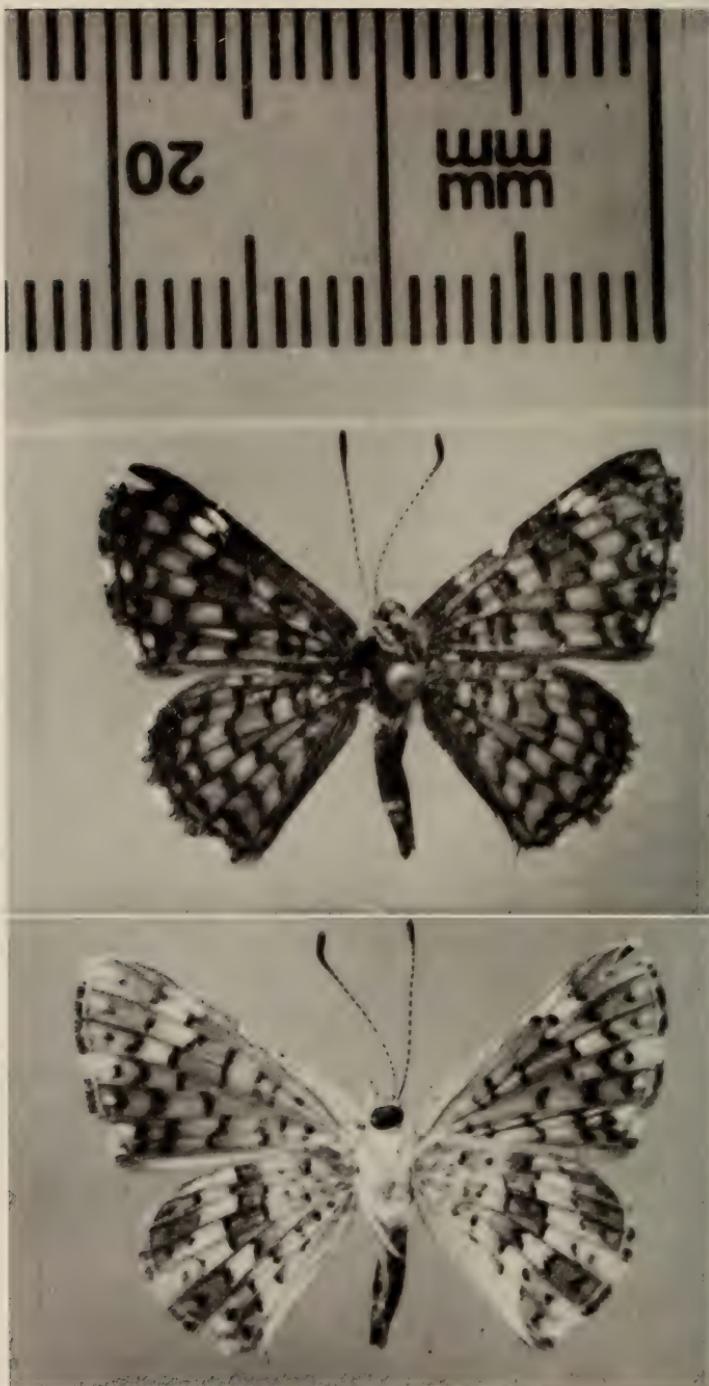
From Fig. 1 we may also note that other ranges (Animas Mountains and the nearby Peloncillo Mountains) are much closer to the present range of *phyciodoides* than the Chiricahuas and have not been so intensively collected. Searches might also focus more profitably on the southern end of the Chiricahua range. Possibly, more intensive work in Mexico might yield habitat-foodplant information that will enable us to rediscover the species in the southwestern United States.

LITERATURE CITED

BARNES, W. & F. H. BENJAMIN. 1924. Contributions to the Natural History of the Lepidoptera of North America, 5:99–100.
CLENCH, H. 1955. A collection of butterflies from western Chihuahua, Mexico. Ent. News, 76:157–162.
HOLLAND, R. 1974. Butterflies of six central New Mexico mountain ranges, with notes on *Callophrys* (*Sandia*) *macfarlandi* (Lycaenidae). J. Lepid. Soc., 28:38–52.
HOLLAND, W. J. 1900. A description of a variety of *Argynnis nitocris* from Chihuahua, Mexico. Ent. News, 11:332–333.
LOWE, C. H. 1964. Arizona's Natural Environment. University of Arizona Press, Tucson, Arizona. 136 pp.
SCHULMAN, E. 1956. Denduoclimatic Changes in Semiarid Arizona, University of Arizona Press, Tucson, Arizona. 142 pp.

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FIG. 2. *Apodemia phyciodoides* ♂, dorsal and ventral surfaces; 5 mi. NW Colonia Juárez, canyon of Rio Piedras Verdes, 5000′, Chihuahua, Mexico, 28 June 1979, leg. R. Holland.

APPENDIX

Records of *Apodemia phyciodoides*

MEXICO, Chihuahua:

5–6 mi. NW Colonia Juárez, canyon of Rio Piedras Verdes, 5000′: 9 April 1978 (3♂♂)
  RWH, 10 April 1978 (1♂) RWH, 25 June 1979 (3♂♂) GSF, 26 June 1979 (2♂♂)
  GSF, (5♂♂) RWH, 24 Aug. 1979 (1♂, 1 ♀) GSF, 25 Aug. 1979 (1 ♀, 7 ♂♂) GSF,
  11 Sept. 1979 (1♀, 5♂♂) GSF, (1♂) N. J. Miles, 3 April 1980 (2♀♀, 3♂♂) GSF, 4
  April 1980 (3♂♂) GSF, (1♂) S. Judd
9.5 mi. NW Colonia Juárez, 5500′: 10 April 1978 (2♀♀, 1 ♂) RWH
6.5 mi. W Rancho Gavilán, 23.4 mi. E Tres Rios, 5600′ (30°3′N, 108°32′W). 13 April
  1978 (1♂) RWH

  Sonora:

Tres Rios at Rio Bivaspe (29°52′N, 108°38′W) 4800′: 12 April 1978 (5♂♂) RWH, 13
  April 1978 (1♂) RWH
6.2 mi. N of Mesa Tres Rios & 50.3 mi. S of Huachinera on Rio de Los Lobos, 5900′
  (29°41′N, 108°49′W): 1 July 1979 (1♂) B. Harris

BOOK REVIEW

LES ATTACIDAE AMERICAINS. THE ATTACIDAE OF AMERICA (=SATURNIDAE): ARSEN-
URINAE, by Claude Lemaire. 1980. Neuilly-sur-Seine, France: C. Lemaire. 199 pp., 171
figs., 76 pls. (4 in color).

In continuation of the series, *Les Attacidae Americains*, and following publication
in 1978 of volume 1, Lemaire here presents volume 2. This volume treats the entirely
Neotropical subfamily Arsenurinae, encompassing 57 species and including some of
the more spectacular saturniids, as in the genus *Copiopteryx*. As in volume 1, each
species is illustrated full size among the 76 plates, of which 4 are in color. Likewise,
the text continues in the previous manner, with each species text in French followed
by an English summary. Thus, persons not familiar with French can still easily use the
volumes.

Only three new subspecies are described in volume 2. One new tribe is proposed
for the monobasic genus *Almeidaia*.

Technically, this second volume continues Lemaire's excellent coverage. Full syn-
onymies are given for all taxa and all infraspecific names are noted in synonymy.
Lemaire follows priority strictly; thus, adopting the name Arsenurinae over the more
commonly used Rhescyntinae. I found no major errors or misspellings. My only criti-
cism involves the retention of some of the subspecies, inasmuch as they are not geo-
graphically isolated in some cases and may indeed only represent altitudinal forms.
However, the subspecies category is fortunately used sparingly, which can only be
praised when compared to such examples as *Zygaena* and *Parnassius*, where the use
of subspecies has been taken to its most absurd extreme.

We can but welcome this new addition to Dr. Lemaire's continuing revision of the
New World saturniids (or Attacidae) and hope for a short interval for the next volume
in the series to be published.

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ton, D.C. 20560.*

A NEW SPECIES OF *OZAMIA* RAGONOT (PYRALIDAE) FROM TEXAS

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ABSTRACT. *Ozamia multistriatella,* a new species of the subfamily Phycitinae, is described. Imagines, male and female genitalia, and wing venation are figured.

Ozamia multistriatella A. Blanchard & E. Knudson, **new species**

Description: *Head:* Frons clothed with white tipped smokey gray scales. Vertex slightly darker. Maxillary palpi squamous. Labial palpi speckled white and black, exceeding frons by nearly two eye diameters. Antennae simple, whitish gray, bearing, on the male, thorn-like conical tufts of black scales on the first 6 or 7 segments of the flagellum, aligned along the inner surface.

Thorax: Patagia, tegulae, and mesonotum ashy gray.

Forewing (Figs. 1, 2): *Dorsal surface:* Ground color powdery gray, under magnification composed of a mixture of white tipped gray scales, pure white scales, and dark gray scales. Costal third predominantly white, contrasting with the ground. Narrow longitudinal rows of black scales, extending mainly along the veins and most evident in the costal third, result in a striated pattern. Antemedial line prominent, black, sharply angled outward over the cell. Subterminal line weak, white, with black inner and outer margins. Small black dash-like discal spot. Fringe light gray. *Ventral surface:* Light brown with whitish speckling near costa.

Hindwing (Figs. 1, 2): Semitranslucent pale luteous, with darker veins and outer margin. Fringe whitish.

Length of forewing: *Males:* (N = 6), 11.8–13.5 mm, average 12.6 mm. *Females:* (N = 8), 11.3–12.6 mm, average 11.9 mm.

Venation (Fig. 9): Forewing with 11 veins, veins Sc and R1 conspicuously widening toward costa. Hindwing with vein M1 absent, veins Cu1 and M2 stalked, and veins Sc and Rs anastamosing more than half the distance from upper corner of cell to margin.

Male genitalia (Figs. 3–6): Uncus conical. Prominent bifid gnathos (Fig. 5), with large rounded anterior, and small posterior processes. The long fork-like juxta is shown together with the aedeagus in Fig. 3. Fig. 4 is of the genitalia with both aedeagus and juxta removed and also showing the separated aedeagus. The ventral tufts and sclerotization of the 8th segment are shown in Fig. 6.

Female genitalia (Figs. 7, 8): Bursa copulatrix very finely scobinate, wrinkled around the plate-like signum. Ductus seminalis arising from bursa near signum. Ductus bursae lightly scobinate along anterior third. 8th segment collar (Fig. 8), broadly and roundly excavated on its dorsal aspect.

Holotype (Fig. 1): Male, Fort Davis, Jeff Davis Co., Texas, 25-III-68, collected by A. & M. E. Blanchard, deposited in the National Museum of Natural History.

Paratypes: Fort Davis, Jeff Davis Co., Texas, 25-III-65, 1 male; same location, 17-V-66, 1 male; Kerr Wildlife Management Area, Kerr Co., Texas, 23-III-65, 1 female; Sierra Diablo Wildlife Management Area, Culberson Co., Texas, 20-V-68, 1 female; same location, 27-V-73, 3 males, 2 females; same location, 29-V-73, 1 female; Big Bend National Park, Green Gulch, Brewster Co., Texas, 28-III-71, 1 female; all collected by A. & M. E. Blanchard. Nickle Creek, Culberson Co., Texas, 26-V-81, 2 females, collected by E. C. Knudson.
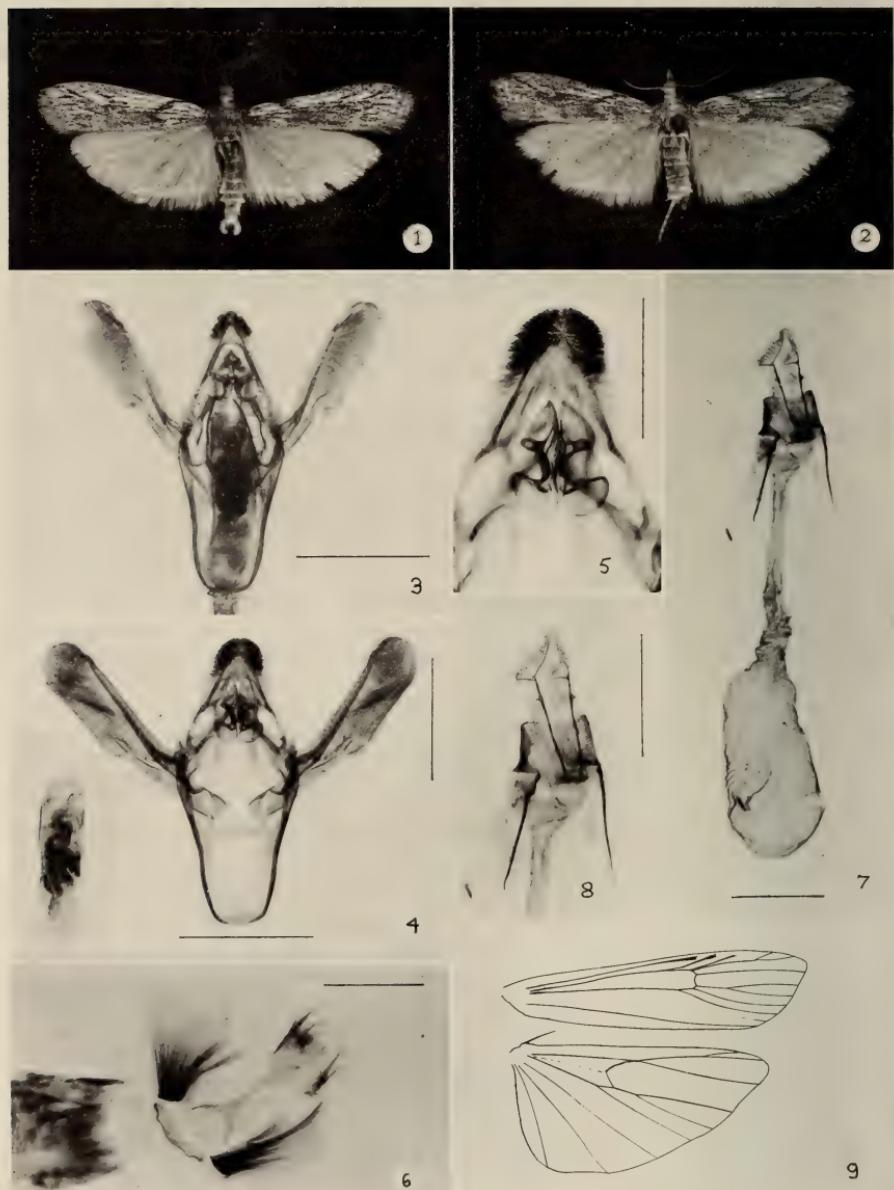
FIGS. 1–9. *Ozamia multistriatella*. **1,** Male holotype. **2,** Female paratype, Sierra Diablo Wildlife Management Area; Culberson Co., Texas, 27-V-73. **3,** Male genitalia of paratype, Ft. Davis, Jeff Davis Co., Texas, 17-V-66, slide A.B. 421. **4,** Male genitalia of paratype, Sierra Diablo Wildlife Management Area, Culberson Co., Texas, 27-V-73, slide A.B. 4969. **5,** Enlargement of part of Fig. 4 to show gnathos. **6,** Hair tufts of 8th abdominal segment, same insect, same slide as Fig. 4. **7,** Female genitalia of paratype, Nickel Creek, Culberson Co., Texas, 26-V-81, slide E.C.K. 148. **8,** Enlargement of part

REMARKS

This new species falls into the genus *Ozamia* Ragonot chiefly by characteristics of the wing venation, genitalia, palpi, and antennae. It is distinguished from its nearest North American relatives, *Zophodia* Hübner, and *Cactobrosis* Dyar, by its simple antennae, maxillary palpi, and female genitalia. Douglas C. Ferguson, who has examined some of the specimens included in the type series, has made the following comment: "This genus is hardly distinct from the South American *Tucumania* Dyar and has the same food plants (*Opuntia* spp.), but the males have simpler antennae. The moths more nearly resemble those of *Tucumania*, especially *T. tapiacola* Dyar, or *Yosemitia* Ragonot, than they do other species of *Ozamia*, or the species of *Zophodia* or *Cactobrosis*."

According to Heinrich (1956), the *Ozamia* fall into two groups; one with a wrinkled bursa copulatrix and densely scobinate ductus, and the other with a smooth bursa and naked or lightly scobinate ductus. The former group is mainly tropical, the latter is temperate. *Ozamia multistriatella* seems to occupy a neutral position, possessing as it does, a wrinkled bursa, but lacking the densely scobinate ductus. This would seem to support Heinrich's conclusion that the two groups should not be placed in separate genera.

LITERATURE CITED

HEINRICH, CARL. 1956. American Moths of the subfamily Phycitinae, U.S.N.M. Bulletin 207, Washington, D.C., 1–581.

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of Fig. 7 to show ovipositor and 8th segment. **9,** Venation of male paratype, Sierra Diablo Wildlife Management Area, Culberson Co., Texas, 27-V-73, slide A.B. 4968. (The line scales in Figs. 3, 4, 6, 7, and 8 represent 1 mm; in Fig. 5 the line scale represents 0.5 mm.)

FIFTH ADDITION TO THE SUPPLEMENTAL LIST OF MACROLEPIDOPTERA COLLECTED IN NEW JERSEY

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ABSTRACT. Nineteen species and subspecies and five named infrasubspecific variations not recorded in John B. Smith's Report of the State Museum (1910) or in my earlier reports to date (1965, 1968, 1973, 1976, 1979) are added to the list of Macrolepidoptera collected in New Jersey.

Most of the following new additions were collected by the author, Brooke Worth, James Madenjian and the Entomological Department of Rutgers University. Such specimens are in my collection. Checklist numbers and classification for moths are taken from McDunnough (1938), updated to current nomenclature. Butterfly names are from dos Passos (1964). Localities, date and collector are shown. Specimens not followed by the name of collector were taken by the author. Specimens collected at Eldora, Cape May Co., were collected by the author in collaboration with Dr. Worth.

BUTTERFLIES
NYMPHALIDAE

Speyeria Scudder
618 *atlantis atlantis* (Hy. Edwards) (Det. by Austin Platt)
Chester, 30 July 1978.
M. Monica.

MOTHS
ARCTIIDAE

Cycnia Hübner
992 *inopinatus* (Hy. Edwards)
Eldora, 26 May 1978.

CTENUCHIDAE

Ceramidia Butler
fumipennis (Walker)
East Brunswick, 28 October 1979, J. Vastardis.
Ex: pupa on banana; pest on banana.
Antichloris Hübner
viridis Druce

Lebanon, 11 September 1965, Prostak.
At light.

NOCTUIDAE
Noctuinae

Diarsia Hübner
1504 *rubifera* (Grote)
Lakehurst, 6 August, 18 August (no years), Rummel, in Yale Collection. Also recorded by Forbes (1954).
Abagrotis J. B. Smith
1601-1a *crumbi benjamini* Franclemont
Lakehurst, 9 July 1951.

Hadeninae

Scotogramma J. B. Smith
1633 *trifolii* (Rottenburg) form "indistincta" (Tutt)
Pine Brook, 22 June 1979, Rutgers.
form "albifusa" (Walker).
Short Hills, 22 July 1941.
Lacinipolia McDunnough
1738 *renigera* (Stephens) form "infecta" (Walker)
Lebanon, 5, 20 September 1978.
Leucania Ochsenheimer
1979 *scirpicola* (Guenée)
Hunterdon Co., 20 November 1975.
1989 *junicicola* (Guenée)
Eldora, 10 July 1978.

Amphipyrinae

Oligia Hübner
2420-1 *chlorostigma* (Harvey)
Montvale, 2 July 1979, Rutgers.
Apamea Ochsenheimer
2458-1 *plutonia* (Grote)
Manalapan, 9 June 1978, Rutgers.
2459-1 *nigrior* (J. B. Smith)
Pine Brook, 18 June 1979, Rutgers.
Platysenta Grote
2620-1 *mobilis* (Walker)
Lebanon, 8 October 1978.
Enargia Hübner
2685 *infumata* (Grote)
Chester, 15 June 1979, Rutgers. (det. by Dr. Reed of Rutgers)

ACONTIINAE

Cryphia Hübner
   3100 *villificans* (Barnes & McDunnough)
      Eldora, 12 June 1978.

CATOCALINAE

Catocala Schrank
   3372-1 *carissima* (Hulst)
      Short Hills, 22, 26 July 1941, Wertsville, 24 July 1958.
   3389 *coccinata* Grote
      ab. "chiquita" (Bartsch)
      Edinburg, 6 July 1965, Rutgers.
Phoberia Hübner
   3545 *orthosioides* (Guenée)
      Chatsworth, 12 April 1977, J. Madenjian.
      This species is usually misidentified as *P. atomaris* Hübner.

HERMINIINAE

Epizeuxis Hübner
   3735-1 sp. nr. *concisa* (Walker)
      Eldora, 3 July 1978.

GEOMETRIDAE
GEOMETRINAE

Chloropteryx Hulst
   4102 *tepperaria* (Hulst)
      Eldora, 21 August 1979.

STERRHINAE

Scopula Schrank
   4166 *purata* (Guenée)
      Chatsworth, 19 June 1973, J. Madenjian.
Haematopis Hübner
   grataria (Fabricius)
      f. "annettearia" (Haimbach)
         Hunterdon Co., 17 August 1953, 4 September 1959.
Itame Hübner
   4756a *coortaria enigmata* (Barnes & McDunnough)
      Succasumma, 22 June 1979, Rutgers.

ACKNOWLEDGMENTS

LITERATURE CITED

DOS PASSOS, C. F. 1964. A Synonymic List of the Nearctic Rhopalocera. Lepid. Soc. Mem. No. 1, p. 94.

FORBES, W. T. M. 1954. Lepidoptera of New York and neighboring states, part III Noctuidae. Mem. 329 Cornell Univ. Agric. Expt. Sta., Ithaca, N.Y. 433 pp.

McDUNNOUGH, J. 1938. Check List of the Lepidoptera of Canada and the United States of America, part 1. Macrolepidoptera. Mem. S. Calif. Acad. Sci. 272 pp.

MULLER, J. 1965. Supplemental list of macrolepidoptera of New Jersey. J. N.Y. Entomol. Soc., 73: 63–77.

———— 1968. Additions to the supplemental list of New Jersey macrolepidoptera. J. N.Y. Entomol. Soc., 76: 303–306.

———— 1973. Second addition to the supplemental list of New Jersey macrolepidoptera. J. N.Y. Entomol. Soc., 81: 66–71.

———— 1976. Third addition to the supplemental list of macrolepidoptera of New Jersey. J. N.Y. Entomol. Soc., 84: 197–200.

———— 1979. Fourth addition to the supplemental list of macrolepidoptera of New Jersey. J. Lepid. Soc., 33(3): 174–178.

SMITH, J. B. 1910. Report of New Jersey State Museum for 1909. Trenton.

GENERAL NOTES

LEAF SELECTION FOR OVIPOSITION SITES BY A TROPICAL SKIPPER BUTTERFLY

This communication reports preferential oviposition by a skipper butterfly. *Phocides lilea sanguinea* (Scudder) (Hesperiidae) is a Neotropical skipper which occurs as far north as Brownsville, Cameron County, Texas (Neck, 1978, J. Lepid. Soc., 32: 107–110). All observations of *sanguinea* involve this skipper on strawberry guava, *Psidium cattleianum* Sabine (Myrtaceae) (see Bailey, 1949: 729, Manual of Cultivated Plants, Macmillan, New York), a native of Brazil grown in parts of the United States and Mexico (Standley, 1920–1926: II, 1036; Contrib. U.S. Nat. Mus., 23: 1721 pp.).

While a tremendous amount of data exists in the literature concerning reports of larval foodplants of numerous species of butterflies and skippers, only a small fraction of references refer to the specific plant parts attacked, especially with reference to old vs. new leaves. Little, if any, numerical data concerning intra-plant oviposition discrimination by skippers are available in published form. Practically every temperate zone lepidopterist "knows" that fresh plant growth is preferred by many larval forms. A number of workers (Owen, 1972, Oikos, 23: 200–205; Young, 1972, Psyche, 79: 165–178) have reported that a particular species feeds or oviposits preferentially or exclusively on new growth leaves. One butterfly has even been reported to prefer "young trees" (Muyshondt & Muyshondt, 1976, J. N.Y. Ent. Soc., 84: 23–33). Larvae of the mangrove skipper, *Phocides pygmalion okeechobee* Worthington, were found on "small specimens of red mangrove, *Rhizophora mangle*, which were in heavy shade cast by higher growth" (Strohecker, 1938, Ohio J. Sci., 38: 294–295). However, young leaves are not always the preferred ovipositional substrate. Some tropical heliconians are reported to preferentially oviposit on older leaves (Alexander, 1961, Zoologica, 46: 1–24; Benson et al., 1976, Evolution, 29: 659–680).

On two occasions egg counts of *sanguinea* were made on a single *Psidium* in a residential yard in Brownsville.

On 23 December 1970 a count was made of all leaves on this shrub. Two types of leaves could be differentiated visually at that time. Young leaves exhibited a general yellowish-green coloration with larger veins colored a darker green. Old leaves were a darker green in which veins and matrix were unicolorous.

On 30 November 1975 a second count of *sanguinea* eggs was made. As the selection of terminal leaves for oviposition had already been established, only eggs on these terminal leaves were counted. (A quick perusal of the plant revealed no eggs on non-terminal leaves.) Terminal leaves at this time consisted of three types of leaves. In addition to young and old leaves as previously described, the shrub also contained new leaves. New leaves were generally a rich bronze-green in color; many had not reached full size.

Table 1 contrasts the number of young and old leaves which contained eggs. The results indicate a decided tendency for eggs to be oviposited on young leaves. These data indicate that 92.0% of the eggs were laid on young leaves even though only 51.3% of the leaves on the shrub were classified as young. Further examination of the distribution of *sanguinea* eggs reveals an additional ovipositional discrimination. Leaves of *Psidium* occur in opposite pairs. Eggs found on immature leaves can be further divided into eggs on one leaf of a terminal pair (rarely a single terminal leaf) and eggs on non-terminal leaves. Examination of the data (Table 2) reveals a decided preference for terminal leaves. Although 87.0% of the young leaves with eggs were terminal leaves, only 36.1% of all young leaves are terminal leaves. Only 3.2% of all the leaves of this shrub contained a *sanguinea* egg while 12.8% of the terminal leaves contained eggs.

Few eggs were present on 30 November 1975, but four of the five eggs were on new leaves. No eggs were found on old leaves. At this same time seventeen early-instar larval retreats (see Neck, op. cit.) were located (most were associated with egg shell remnants); all were on new leaves. If one adds these larvae to the egg count, the difference is very significant (Table 3). Therefore, not only do adult females almost

TABLE 1. Eggs of *Phocides lilea sanguinea* on young and old leaves of *Psidium cattleianum* on 23 December 1970.

Leaf type	Leaves with no eggs	Leaves with eggs	Total
Young	376	23	399
Old	376	2	378
Total	752	25	777

$\chi^2_{(1)} = 32.9$; $P \ll .001$.

exclusively oviposit on terminal leaves, but new leaves are preferentially chosen over older leaves.

Additionally, the data collected on 23 December 1970 can be examined to determine whether there is any tendency for females to oviposit on leaves which do not already contain eggs. Of the twenty-five leaves which contained eggs only two contained two eggs; no leaf contained more than two eggs. The observed two-egg-leaf frequency is 0.0026 (2 double-egg leaves of 777 total leaves), while the expected value, assuming leaf selection random with respect to presence/absence of egg, is 0.0012 (27 eggs on 777 leaves squared); this difference is not significant (d = 1.17; P = .24). These data do not indicate a significant tendency for ovipositing females to avoid laying an egg on a leaf which already contains an egg.

Preference for terminal leaves by *sanguinea* for oviposition sites could result from several factors. Larvae may be able to assimilate material from young, and/or new leaves more efficiently because of reduced levels of toxic phytochemicals as is known for other lepidopterans. Larvae of the winter moth (Geometridae: *Opherophtera brumata* (L.)) are known to gain more weight on new growth than old growth of oaks (Feeny, 1970, Ecology, 51: 565–581). Mature leaves are unacceptable, because high levels of tannic acids are produced following attainment of full leaf size. The general assumption is that immature leaves are more palatable due to low levels of deterrent and/or poisonous phytochemicals. This lower level allows more rapid development, decreasing the larval period with attendant exposure to parasites and predators. Larvae reared on immature leaves tend to be of greater weight which would seem to allow greater fecundity.

An argument might also be made that the rigid ovipositional behavior sequence of *sanguinea* as described previously leads to selection of terminal leaves simply because they are more accessible to quick ovipositional dips onto the foodplant. However, the behavioral choice of these leaves would be the result of natural selection because of increased survival of eggs placed on these leaves. The behavioral sequence is the result of a need to oviposit on new leaves; the choice of new leaves is not the result of a pre-determined ovipositional sequence. Newman & Clark (1926, Austral. For. J., 9: 95–99) reported that the jarrah leaf miner moth (Incuvariidae: *Perthida glyphoga* Common) preferentially oviposits in leaves near the ground, because adults laid eggs

TABLE 2. Distributions of eggs of *Phocides lilea sanguinea* on young leaves of *Psidium cattleianum* on 23 December 1970.

Leaf type	Leaves with no eggs	Leaves with eggs	Total
Terminal	136	20	156
Non-terminal	240	3	243
Total	376	23	399

$\chi^2_{(1)} = 21.3$; $P \ll .001$.

TABLE 3. Distribution of eggs and larvae of *Phocides lilea sanguinea* on terminal leaf pairs of *Psidium cattleianum* on 30 November 1975.

Leaf type	Without eggs or larvae	With eggs or larvae	Total
Young	65	1	66
New	23	21	44
Total	88	22	110

$\chi^2_{(1)} = 32.4$; $P \ll .001$.

on the first suitable leaves discovered and tended to remain in the lower part of the foliage. Subsequently, Wallace (1970, Austral. J. Zool., 18: 91–105) reported numerical data revealing a preference of *P. glyphoga* for younger, more succulent leaves.

Although comparative laboratory and/or field feeding experiments would be required for verification, I believe that placement of eggs on new leaves under growing conditions is an adaptively advantageous site, because such leaves represent a superior nutritive resource. The most efficient method to achieve the above location is to lay eggs on a terminal leaf. Depending upon seasonality of growth of the foodplant, the egg may actually be laid on a new leaf. Jennings (1975, Ann. Ent. Soc. Amer., 68: 1008–1010) reported that females of the southwestern pine tim moth (Tortricidae: *Rhyacionia neomexicana* (Dyar)), preferentially oviposit on leaves of upper crowns of small pine trees. Larvae are then able to locate the nearby growing meristems which provide superior food.

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NOTES ON EARLY STAGES OF *NYMPHALIS CALIFORNICA*
(NYMPHALIDAE)

On 23 March 1972 *Nymphalis californica* (Boisduval) flew abundantly near Alpine Dam, Marin County, California. Two females were collected, and confined in a tub with a small plant of *Ceanothus ramulosis*. On 29 March a stack of pale green eggs was found on the top surface of a leaf near the growing tip of the plant (Fig. 1).

This cluster was about 5 mm across, and near 3 mm high in the center, and suggested a miniature bunch of grapes. Eggs were ovoid, each with eight vertical ribs, which became more prominent where they converged at the apex; diameter was near 0.65 mm; about 40 ova made up the stack.

On 4 April color began to change; on the 5th, ova were blackish, the ridges showing
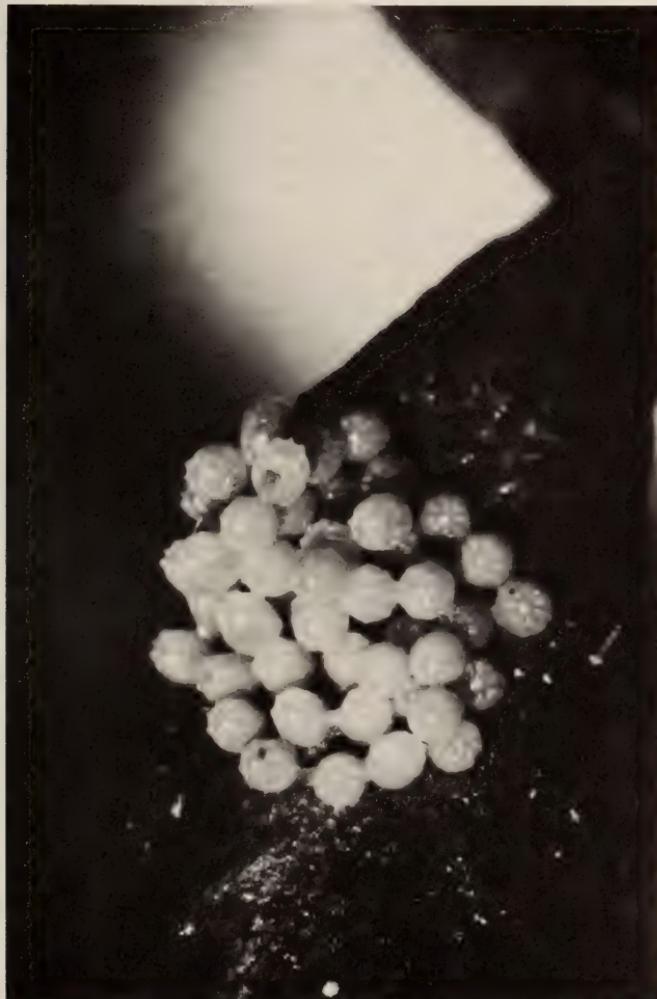
Fig. 1. Cluster of ova of *Nymphalis californica* on leaf of *Ceanothus ramulosis*. (Enlarged 10×.)

as white tracery. That evening hatching began. By morning most larvae were out. Young caterpillars were dull green, sparsely clothed with hairs, with very large, shiny black heads. Their length was between 1.5 and 2 mm. By 1300 on 6 April, most were crowded together on a small leaf just below the terminal bud and had eaten holes there. Next morning it was found that they had covered two leaves and the terminal bud with webbing. On this day the group was observed jerking the fore parts of their bodies in unison in a semicircular motion at a 2-second interval. This motion may have been provoked by some sound or vibration, but nothing was touching or approaching them.

On 8 April the colony moved to a new location and moved again on the 9th. Each time, after completely devouring the surface of 4 to 6 leaves, they crawled down the stem about 4 cm lower, leaving silk as they went, and gathered and began to eat again.

On 10 April the larger of the larvae were about 4 mm long; green with darker shading of thoracic and posterior segments. Each segment was marked dorsally with what resembles a colon and a dash (:—), laterally with a blackish square. On 11 April most of the larvae were pausing for the first moult; by 1600 some had completed this. Second instar larvae still had shiny black heads and green body color, darker at the ends. There was a dorsal line of black dots and dashes; the dots were tubercles, and from them, and two rows of black tubercles on each side, sprang tufts of bristles. During 2nd instar the larvae were transferred to twigs of cultivated hybrid *Ceanothus*.

On 15 April some were 8 mm in length. By morning of the 17th some had passed the 2nd moult; color was now black except for a greenish dorsal stripe with a central line of black dashes extending through segments 4–10. From the tubercles arose short spines with a little branching at the ends.

By 22 April some had passed the third moult. Spines were longer and more branched. By the end of this (the 4th) instar the gregarious habit had been abandoned.

Larvae of the 4th and 5th instars have been described in detail by Henry Edwards (1875, Proc. Cal. Acad. of Sciences, ser. 1, 6: 146–149.), and extracts from these descriptions are repeated in many later works. To those descriptions I will add only that color varied considerably, even in caterpillars of the same brood. Many were velvety black, with a blue glint at base of tubercles, and white hairs scattered over the body, giving a frosted appearance. Some had yellow dorsal patches, and in some a part of the spines were yellow.

On 3 May larvae began to hang up for pupation, and late in the month butterflies emerged; thus, the cycle from oviposition to eclosion covered about two months. In the warmer habitats, which the species frequents, the cycle would be shorter.

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PLUSIINAE (NOCTUIDAE) AT FLOWERS

Literature on Lepidoptera rarely elaborate on the actual methods employed in capturing moths, especially Plusiinae. Most collecting for noctuids involves trapping, utilizing ultraviolet or mercury vapor lights, or bait; however, my experiences with these methods have resulted in relatively few captures of plusiines over my years of collecting in Michigan. I first became acquainted with some of the northern Plusiinae in 1952, while collecting moths at Joe-Pye weed flowers, *Eupatorium* sp., at dusk (with the aid of a flashlight and cyanide jar) at Copper Harbor, Keweenaw County, Michigan. According to the late Sherman Moore (personal communication), many of the Plusiinae taken at that time were either new county records or only the second record for the state. It was this experience that revealed to me that collecting at flowers could be very productive for Plusiinae; but, it wasn't until the late 1960's that I again tried this method of collecting these interesting moths in northern Michigan. The work of Dr. Thomas D. Eichlin also inspired me to make a special effort to collect plusiines and attempt to learn more of their habits and ecology. From 1969 to 1977 I collected these elusive moths at flowers over a total of 30 evenings in four widely separated northern Michigan counties: Chippewa, Keweenaw, Otsego, Schoolcraft.

My collecting experiences extended from 17 July to 6 August, with most of the collecting occurring during the last week of July. I found the most productive period each evening to extend from approximately 2045 to 2215 EDST, although some loopers appeared at 2030 and probably continued to fly later than the time I spent there. Plusiinae activity at flowers began to decrease after 2230.

In each of the above counties, I located a good stand of fireweed, *Epilobium angustifolium* L., in close proximity to sphagnum-heath bogs or in open pine and aspen forests. In all locations there was the presence of spruce, either *Picea glauca* (Moench) Voss or *P. mariana* (Mill.); fir, *Abies balsamea* (L.) Mill.; *Vaccinum* sp.; willow, *Salix* sp. and miscellaneous shrubs, plus herbaceous plants, all possible foodplants for many of recorded species (Table 1). Most of the fireweed patches were along a trail or sandy road, affording easy access for moving about on foot. I used a head-mounted flashlight, an aerial nylon net with a three foot handle and at least three large-mouth cyanide jars. Once I had determined where to stand and watch, the cyanide jars were placed on the ground within easy reach. I had no difficulty seeing the buzzing moth as it darted from flower to flower at dusk, but needed the flashlight when it got too dark. As each moth was netted, I quickly snapped the net to the ground and inserted a cyanide jar up into the net, sometimes using the flashlight to locate the struggling moth in the net. Unless one's actions were swift and accurate, the moth was apt to be 'scalped' on the thorax and rubbed on the wings! I discovered it was best to remain motionless until the first moth was spotted, as plusiine moths are extremely wary and will dart off at the slightest noise or movement. Mosquitoes constantly buzzing around my head and eyes made standing still even more difficult! As the evening grew darker, I had problems judging distance, and consequently, missed several moths that looked like easy catches. I collected under all kinds of weather and temperature conditions, but had the most success under cloudy skies with temperatures at least 60°F. A total of 43 Plusiinae specimens were collected in one evening during a light rain, which is similar to an observation reported by Eichlin and Cunningham (1978, Tech. Bull. No. 1567, USDA). Some of the other flower species frequented by Plusiinae at these locations included: *Apocynum androsaemifolium* L., *Asclepias syriaca* L., *Centaurea maculosa* Lam., *Cirsium* sp., *Diervilla Lonicera* Mill., *Eupatorium* sp. Usually, some of these flowers were found close to the fireweed patches; the taller fireweed plants in larger numbers made them ideal nectaring targets for resident Plusiinae.

The highest number of target species taken on any night was 10, with *Chrysanympha formosa* (Grt.) and *Syngrapha rectangula* (Kirby) being the two most common species found at each location. Four of the species collected were new state records: *S. altera* (Otto.), *viridisigma* (Grt.), *abstrusa* and *cryptica*. The latter two species were recently described by Eichlin and Cunningham (1978, ibid.), while *viridisigma* was elevated from the synonymy of *selecta* (Wlk.), by the latter authors. Most of the previous Michigan

TABLE 1. Results of collecting Plusiinae at flowers in northern Michigan, from 17 July to 6 August: a 6-year period extending from 1969 to 1977.

Species and (number collected)		Hosts**						
		1	2	3	4	5	6	7
Plusia balluca (Geyer)	(6)		X		X	X		
Allagrapha aeroides (Grote)	(28)			X	X		X	
Pseudeva purpurigera (Walker)	(2)			X	X			
Chrysanympha formosa (Grote)	(50)				X		X	
Eosphoropteryx thyatyroides (Guenée)	(2)				X			
Autographa precationis (Guenée)	(9)				X			
A. bimaculata (Stephens)	(34)	X		X	X	X		
A. pseudogamma (Grote)	(2)				X			
A. mappa (Grote and Robinson)	(3)						X	
A. ampla (Walker)	(6)			X	X		X	
*Syngrapha altera (Ottolengui)	(1)				X			
*S. octoscripta (Grote)	(20)			X	X			
*S. epigaea (Grote)	(25)				X			
*S. selecta (Walker)	(1)				X			
*S. viridisigma (Grote)	(32)	X		X	X			X
*S. alias (Ottolengui)	(37)	X		X	X			X
*S. abstrusa Eichlin and Cunningham	(2)				X			
*S. cryptica Eichlin and Cunningham	(6)				X			
S. rectangula (Kirby)	(56)				X		X	
Chrysaspidia putnami (Grote)	(7)				X			
(20 species) Total specimens collected 329								

* Specimens determined by T. D. Eichlin.
** 1. *Apocynum androsaemifolium*, 2. *Asclepias syriaca*, 3. *Centaurea maculosa*, 4. *Epilobium angustifolium*, 5. *Cirsium* sp., 6. *Diervilla Lonicera*, 7. *Eupatorium* sp.

records of *selecta*, as cited by Moore (1955, Misc. Pub. Mus. Zool., U. of Mich., No. 88), refer to *viridisigma*. A total of 20 species of Plusiinae were collected during this period at flowers, largely fireweed. As expected, the moths collected in this region have ranges which have been categorized generally as Nearctic Boreal.

Fireweed flowers appear to be the most attractive to many Plusiinae in northern Michigan. I believe collecting at these and other flowers, plus collecting both earlier and later in the season, could result in the capture of additional plusiine species and contribute to the distributional knowledge of these handsome and fascinating moths. It is hoped that these observations and experiences will stimulate other collectors to consider collecting Plusiinae at flowers.

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TWO NOTABLE RANGE EXTENSIONS FOR *CALLOSAMIA SECURIFERA*
(SATURNIIDAE) IN GEORGIA AND SOUTH CAROLINA

Probably no other native moth has attracted so much attention in the past twenty years as *Callosamia securifera* (Maassen). Its geographical distribution is still only poorly known, partly because the species was not well understood until recently, having been ignored or treated as merely a subspecies of *Callosamia angulifera* (Walker), and partly because the coastal plain areas of the southeastern United States, where it occurs, have not been well collected. Peigler (1976, J. Lepid. Soc., 30: 111–113) described how to collect cocoons of *C. securifera* and summarized the known distribution (1975, ibid., 29: 188–191). Pertinent to the records described below is a map presented by Peigler (1975) showing not only the documented areas in which the species has been found, but also hypothetical areas postulated on the basis of correlations of the distribution of the food plant, sweetbay, *Magnolia virginiana* L., with elements of the Floridian flora that spread northward and westward on the Coastal Plain.

During botanical field work on 17 February 1980, in company with Earl Parker and Florence and Raymond Givens, the senior author discovered two unmistakable cocoons of *C. securifera* in Turner County, Georgia, near where Interstate 75 crosses the west fork of Deep Creek, 14.5 km north of Ashburn. The habitat is an extensive open swampy area west of the highway dominated by hundreds of young saplings and trees of bald cypress, *Taxodium distichum* (L.) Richard, most of them less than 5 m tall. Here numerous young trees and shrubs of sweetbay are scattered over an area of about 0.8 km². On the date of the visit, the foliage of sweetbay was still green and attached. The first cocoon was wrapped in three leaves drawn together longitudinally and was found at the tip of a leader shoot about 2 m high. The second cocoon had lost its surrounding leaves except for part of a brown leaf blade on one side and was hanging from a branch about 3 m high. Both cocoons were pale silver in color, with a compact, hard central cell and a very loose, soft outer covering, in contrast to the typical pendent cocoon of the common *C. promethea* (Drury), which is usually darker, much smaller, and with little differentiation between the inner cell and the outer covering. Cocoons of *C. securifera* were figured by Jones (1909, Entomol. News, 20: 49–51, pls. 3, 4). A typical male emerged from one of the cocoons during the following summer.

This new locality is the third for this rare species in Georgia and is over 150 km west of the previously reported ones in Long Co. and the Okefenokee Swamp. More importantly, the place is nearly 130 km north of Peigler's documented area of 1975 (fig. 1), being at the extreme north edge of his hypothetical area, thus, confirming the postulated inland extent of *C. securifera*. Indeed, this is evidently the most inland site ever reported for this species, being almost 190 km from the nearest shore of the Gulf of Mexico.

Another significant record, previously unpublished, is Screven Co., Georgia. A female from this county taken 20 May 1946 by Otto Buchholz is in the American Museum of Natural History in New York City. The correct determination of the specimen was verified by the junior author.

Still another notable range extension was reported to us by John W. McCord, who discovered three cocoons of *C. securifera* in his yard a few kilometers southeast of Manning, Clarendon Co., South Carolina. This record is not only a new county record but a major range extension inland for that state.

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THE OCCURRENCE OF *NOCTUA PRONUBA* (L.) (NOCTUIDAE) IN NOVA SCOTIA: A NEW NORTH AMERICAN RECORD

A male *Noctua pronuba* (L.) was captured on 8 August 1979 under a house porch light in west end Halifax, Nova Scotia. The specimen was in somewhat worn condition. Whether its occurrence was the result of an individual introduction or indicative of an established breeding population cannot be determined at this time.

Noctua pronuba is a widespread Palearctic species. The larva has been recorded as feeding on a wide variety of plants, including *Poa annua* L., *Rumex, Polygonum, Atriplex, Myosotis* and *Taraxacum* species, and various Cruciferae (Beck 1960, Die Larvalsystematik Der Fulen, Akademic-Verlag, Berlin, p. 148). In Britain the larva is sometimes a pest in flower and vegetable gardens (South, 1972, The Moths of the British Isles, Warne, London, p. 163).

This specimen, which is in my collection at Dalhousie University, Halifax, represents the first known record of *Noctua pronuba* for North America. A photograph of the specimen (Fig. 1) is given.

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Fig. 1. *Noctua pronuba* L. Male from Armdale, Halifax, Nova Scotia, 8 August 1979, K. Niel (3.5×).

OBITUARY

Hardin Blair Jones, 1914–1978

Hardin Blair Jones, who was Professor of Medical Physics, Professor of Physiology, and Assistant Director, Donner Laboratory, University of California, Berkeley, held a keen avocational interest in butterflies and assembled a collection that has now been deposited with the California Academy of Sciences. He was born in Los Angeles, California, on 11 June 1914, to Maude Blair and Hardin Henry Jones, and died after a brief illness on 16 February 1978, in Berkeley, California. His educational and professional life centered around the University of California, where he received the A.B. at the Los Angeles campus in 1937, and the M.A. in 1939 and the Ph.D. in 1944 at the Berkeley campus. His dissertation was based on one of the early applications of radioactive tracers in metabolic studies. He was appointed Assistant Professor of Physiology at Berkeley in 1947 and advanced to Professor in 1954, with a concurrent appointment in the Division of Medical Physics of the Physics Department. Details of his contributions are discussed in an "In Memoriam" by Cornelius A. Tobias, Daniel I. Arnon, John H. Lawrence, and Paola S. Timiras of the University of California, Berkeley, published in September 1978, and from this is quoted:

> "In his contacts with students Jones became aware of an increasing indulgence in hallucinatory drugs. The contradictions between scholarly pursuits and mental abuse by drugs troubled him and led to an exhaustive study of the drug question and the characteristics of users of sensual drugs worldwide. A course of instruction he developed on the use and abuse of drugs proved extremely popular. His publications and lectures on this subject culminated in a book, *Sensual Drugs: Deprivation and Rehabilitation of the Mind*, coauthored by his wife, Helen Cook Jones. Jones scientific bibliography totaled 140 publications."

In recent years, he was probably best known among laymen for his drug abuse research and for his stand against the use of marijuana.

Hardin Jones began his interest in Lepidoptera with the aid of a biology teacher at Glendale High School. He collected in the desert areas of southern California with his brother, Jordan L. Jones and an uncle, Leon Sanborne. In his college years he visited with Lloyd L. Martin and Dr. John A. Comstock at the Los Angeles Museum (now the Los Angeles County Museum of Natural History). This is from information supplied by Mr. Martin (from a telephone conversation to PHA on 3 July 1980), who recalls his very fine, friendly personality. Jones also attended meetings of the Lorquin Entomological Society, but a "Directory of members of the Lorquin Entomological Society and a brief historical sketch of the organization, Los Angeles, California, November 1940, 8 pages" authored by John A. Comstock does not list him as a member (probably because he did not reside in the area, since he was a graduate student at the University of California, Berkeley). In southern California his associates also included "Padre" Loye Miller, an ornithologist; J. D. Gunder; Albert and Amy Carter, the owners of a Butterfly Park in Roscoe (now called Sunland); and Dr. Clemence of Atascadero. Special collections were made in the Atascadero area; and also in the San Gabriel Mountains for forms of the California dog-face butterfly. With his move to the Bay Area to attend the University of California, Berkeley, and with subsequent university responsibilities, his collecting became inactive. The collections made in this period were donated to the Los Angeles County Museum of Natural History between the mid-thirties through 1940, and it is recalled by his brother Jordan that portions were placed on public display at that time, probably with other museum material.

His enthusiasm for collecting was rekindled in the 1950's on business and vacation trips with his family. His daughter Carolyn Jones reports that he was rarely without his collapsible net and collecting jar that accompanied him on his travels throughout the world. Representative localities and dates at which some collections were made

HARDIN BLAIR JONES, 1914–1978

include: at Antigua, Guatemala, in March 1957; at Hardin Flats,[1] Tuolumne County, California, in June 1957; at Bishop Creek, Inyo County, California, in July 1957; at Catalina Island, California, in September 1957; at Puerto Vallarta, Mexico, in December 1957 and 1959; at Lafayette, Contra Costa County, California, in March–May and August 1960; at Mitchell Canyon, Contra Costa County, California, in May 1960; at Swan River, Flathead County, Montana, in July 1960; at Grand Teton National Park, Wyoming, in August 1960; at Glacier National Park, Montana, in July 1961 and 1962; and at Yosemite National Park, California, in June 1962; at Wells, Nevada, in June 1965; at Mazatlan, Mexico, in December 1970; and at Katmandu, Nepal, in March 1973.

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[1] We are aware of three spellings used for this name, and we follow the spelling that appears on the California State Automobile Association map "Yosemite National Park and part of the San Joaquin Valley" and the road signs in the area. Other orthographies are "Harden Flat" found on the U.S. Department of the Interior Geological Survey map of the Lake Eleanor quadrangle, California, 1946, and "Hardins Flat" discussed on page 127 in California Place Names, by Erwin G. Gudde, 1960, Second edition, University of California Press, Berkeley and Los Angeles, pp. [i–xiii], 1–383.

Portions of these collections were stored in 27 glass-topped drawers that formed part of a counter in his home study and in wall mounts, and they were available for study and for display to visitors. It was these more recently acquired collections that were donated to the Department of Entomology, California Academy of Sciences, by his widow, Helen Cook Jones, and through the interest of his daughter, Carolyn F. Jones. The donation consisted of 2587 specimens of which 2241 were collected in the United States and 346 are of exotic origin. Each specimen of this donation will carry a label that reads "HARDIN BLAIR JONES/ COLLECTION/ 1978–1980 Gift to/ CALIFOR-NIA ACADEMY/ OF SCIENCES."

Lepidoptera can be a rewarding avocation, providing an aesthetic and relaxing pleasure, as in this instance, to an otherwise very busy professional life, and yet lead to a contribution to the fund of entomological knowledge through an accumulation of properly documented specimens that will be utilized by others in research in future years.

Another avocational interest in Dr. Jones' life was Asian Art. This interest led to his appointment as an Asian Art Commissioner to the Avery Brundage Collection of the de Young Museum, San Francisco, during the years 1974–1977.

Hardin Blair Jones is survived by his wife, Helen Cook Jones of Berkeley, California, and 4 children—Carolyn Frances Jones of Menlo Park, Dr. Hardin Cook Jones of Los Altos, Nancy Jones Snowden of Saint Helena, and Mark Blair Jones of Oakland, five grandchildren, a sister Betty J. Westen of Walnut Creek, and a brother Jordan L. Jones of Huntington Park.

We are indebted to Mrs. Helen Cook Jones, Ms. Carolyn F. Jones, Mr. Jordan L. Jones, Ms. Gay C. Hunter, Dr. Charles L. Hogue, Mr. Lloyd L. Martin, and Mrs. Jacqueline Schonewald for information contained in this report.

PAUL H. ARNAUD, JR. & THOMAS W. DAVIES, *California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.*

BATES, BEETLES, BUTTERFLIES, BIOLOGY AND BOOKS: A BOOK REVIEW

THE PRINCIPAL CONTRIBUTIONS OF HENRY WALTER BATES TO A KNOWLEDGE OF THE BUTTERFLIES AND LONGICORN BEETLES OF THE AMAZON VALLEY. Edited by E. Gorton Linsley, with an introduction by Kier B. Sterling. Arno Press, 3 Park Avenue, New York, N.Y. 10016. December 1978. List price (Hardback) $50.00. ISBN 0-405-10690-4.

This book is introduced by a two-page summary of the life of Henry Walter Bates (1825–1892), written by the editor of the Arno Press Collection "Biologists and their World"; the collection includes 55 volumes as of the printing of this one, mostly on fish, reptiles, birds and mammals, with a few on plants and six others on invertebrates (including works of G. M. Wheeler, C. V. Riley, T. Say, J. Richardson, and J. L. Le-Conte). This is followed by simple photographic reprints, with one exception without accompanying plates (and in the exception, the colored plates of the original are extremely poorly rendered in black and white), of a total of 12 papers readily available in nineteenth century British journals, as follows:

A. An obituary sketch of Bates written by David Sharp, in The Entomologist, 25: 77–80 (April 1892).

B. Eleven of the most important of Bates' works on butterflies and longicorn beetles:

1. Notes on South American butterflies. Trans. Ent. Soc. London, 5: 1–11 (1859). Treats systematics, evolution, and natural history of *Papilio, Heliconius,* Ithomiinae, *Agrias, Callithea, "Cybdelis" pharsalia* (recognized as a new genus, later to be named *Antigonis* by Felder), *Caerois,* Theclinae, *Mesosemia,* and many other Riodininae including early stages.

2. Contributions to an insect fauna of the Amazon Valley. Part I. Diurnal Lepidoptera. Trans. Ent. Soc. London, 5:223–228 (1859) and 335–361 (1861). Discusses biogeography and the Papilionidae.

3. Contributions to an insect fauna of the Amazon Valley. Lepidoptera—Papilionidae. J. Entom., 1: 218–245 (1861). Gives a 5-family classification of Rhopalocera [Hesperiidae, Papilionidae (including Papilioninae and Pierinae), Lycaenidae, Erycinidae (including Libytheinae), and Nymphalidae (including Nymphalinae which subtends the Nymphalinae, Ageronidae, Eurytelidae and Morphidae of others, Brassolinae, Satyrinae, Danainae, Heliconinae, and Acraeinae)], and discusses all the Papilioninae and Pierinae of the Amazon Basin, with notes on natural history.

4. Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. Trans. Linn. Soc. London, 23: 495–566, 4 plates (1862). A famous paper in which the phenomenon of mimicry is proposed, defined, and extensively discussed, with abundant examples and particular reference to dismorphiine ("*Leptalis*") mimics of heliconians and ithomiines (as "Danaoid Heliconidae"), and to evolution and natural selection. In the systematic list, Bates describes two genera and 28 species of Ithomiinae, 5 of Riodininae (all in the new genus *Ithomeis*), and 8 of Heliconiini.

5. Contributions to an insect fauna of the Amazon Valley. Lepidoptera—Nymphalinae. J. Entom., 2: 175–213 (1864). Justifies the higher classification proposed in 1861, especially through larval characters, and discusses 73 species from *Colaenis* through *Pandora,* including *Eunica* and Callicorini but not any Charaxinae; describes 15 new species. The reprinting did not include Plate IX, which figures four new *Eunica* and one new *Eresia.*

6. On the blue-belted *Epicaliae* of the forests of the Amazons. Entom. Monthly Mag., 2: 174–177 (1866). Discusses habits and relations of *Nessaea ancea (obrinus* auctorum), *N. hewitsonii,* and *N. batesii,* describing the female of the last.

7. Contributions to an insect fauna of the Amazon Valley. Coleoptera: Longicornes. Ann. Mag. Nat. Hist., 8: 40–52, 147–152, 212–219, 471–478 (1861); 9: 117–124, 396–405, 446–458 (1862); 12: 100–109, 275–288, 367–381 (1863); 13: 43–56, 144–164 (1864); 14: 11–24 (1864); 15: 213–225, 382–394 (1865); 16: 101–113, 167–182, 308–314 (1865); 17: 31–42, 191–201, 288–303, 367–373, 425–435 (1866). A summarily important monograph giving descriptive, biogeographical, and biological notes on the Lamiinae of the Amazon Basin, including description of 36 new genera and 312 new species (49 in *Colobothea* alone, and 28 and 23 in the new genera *Nyssodrys* and *Lepturges,* respectively).

8. New genera of *Longicorn Coleoptera* from the River Amazons. Entom. Monthly Mag., 4: 22–28 (1867). Describes 14 genera of Cerambycidae.

9. Contributions to an insect fauna of the Amazon Valley (Coleoptera, Prionides). Trans. Ent. Soc. London, 1869: 37–58 (1869) (Bates was then President of the Entomological Society). Catalogues the 26 Prioninae (which include the gargantuan *Macrodontia cervicornis* and *Titanus giganteus*) of the Amazon Basin, of which 8 are newly described, along with one species from Mendoza and three from Central America.

10. Contributions to an insect fauna of the Amazon Valley (Coleoptera, Cerambycidae). Trans. Ent. Soc. London, 1870: 243–335, 391–444 (1870). Discusses an additional 320 species of Cerambycidae (of which 94, and 13 genera, are newly described), using Lacordaire's new classification for the family. Gives a tabular summary, by subfamily, of the 221 genera and 679 species of longhorn beetles in the Amazon.

11. Notes on the Longicorn Coleoptera of tropical America. Ann. Mag. Nat. Hist. [2], 11: 21–45, 117–132 (1873). Discusses natural history and mimicry of a variety of genera, including description of 14 species of *Ommata,* 9 of *Odontocera,* 2 each of *Achyphoderes, Isthmiade,* and *Charis* (the last is a homonym of a riodinine butterfly genus), and one each of *Tomopterus* and five new genera.

Upon perusal of this valuable collection of papers, there remains no doubt that Bates was among the most perceptive, thorough, careful, and pioneering biologists of his

time. It is now also widely recognized that he was one of the most important elements in the early testing, application, and propagation of Darwin's ideas on natural selection. The papers reprinted in this volume show that Bates' work on the Amazon insect fauna represented a fundamental contribution to the Darwinian school of biological thought, which was soon to be assailed by a multitude of detractors from both within and without the scientific world of the late nineteenth century. The papers also bear testimony to Bates' scholarship and detailed taxonomic and morphological research, as well as the excellence of his field work.

Modern scholars of the history of science, of Neotropical butterflies and longicorn beetles, of the development of mimicry theory, and of biogeography should unquestionably profit from familiarity with these papers of Bates. It is thus most unfortunate that this collection is priced far above the cost of copying these 11 papers on machines available in any good library, which is likely to have all these papers (352 double pages = $17.60; only 100 pages deal with Lepidoptera = $5.00). Thus, the sales of the book are likely to be strongly restricted to a few libraries and specialized workers, who feel a need to have these papers together in a single bound volume for easier reference. The Arno Press could probably sell thousands of a paperback version priced under $15.00, especially should they advertise through Entomological Reprint Specialists and various entomological journals; I hope that they will consider thusly, making available this important collection.

It is also most unfortunate that the book omits original plates, and does not include a few essays by modern students of Bates' contributions to biological science, which could analyze his field work, his evolutionary thought, his views on mimicry and biogeography, and his enormous work on the natural history of the Amazonian fauna. They might also analyze his famous prediction in "The Naturalist on the River Amazons," when, after a complex justification based on evolution, ecology, ontogenesis and morphology, he states that "The study of butterflies—creatures selected as the types of airiness and frivolity—instead of being despised, will some day be valued as one of the most important branches of Biological science." Bates is surely the godfather of the many modern evolutionary biologists who use butterflies as experimental animals to study natural processes in the field and the laboratory, and he is a worthy one. But has Bates' "some day" come any closer?

Many people today ask why Bates, after his sojourn on the Amazon and his famous writings on mimicry, natural selection, ecology, geography, and anthropology, settled down and spent the rest of his research career developing "mere taxonomy" of butterflies and beetles. People asked this question of Bates in his own time, also. As a modern-day Amazon sojourner for the same period (eleven years) who, like Bates, has received enough new material to work on for the rest of my life, I can fully agree with Bates' own reply as to why he offered the world no further "wide generalizations or ingenious suggestions" after his paper on mimicry (1862). Commenting on the immensity of the descriptive work to be accomplished and the comparatively small progress made on it by entomologists, he said in one of his Presidential addresses to the Entomological Society, "Thus, our best working entomologists are led to abandon general views, both from lack of time to work them out, and the consciousness that general views on the relations of forms and faunas are liable to become soon obsolete by the rapid growth of knowledge." As his biographer David Sharp comments, ". . . there can be little doubt that Bates restricted his own work of late years to descriptive entomology, because he felt that it is at the present the form of entomological work that has the most permanent utility."

We now live in a time when no one naturalist could claim to know as much about Amazon insects as did Henry Walter Bates a hundred years ago, and very few would care to. On the other hand, unfounded and unsupported generalizations are cheap and abundant in the literature on Neotropical butterflies, often based on mere snippets of data already commented by Bates in the 1860's. Those who would labor to collect enough descriptive data to test such generalizations (as did Bates), and who like Bates, are prone to discover new and important generalizations, are derided and can find no funds for their painstaking natural history and systematic work. Hopefully, the travels and

career of Bates may help to inspire young entomologists to abandon easy generalizations and "quick and dirty" field experiments in the peripheral Neotropics, and once again penetrate the complex reality of the Amazon Basin. Here, they can still observe and absorb a multitude of new facts and phenomena which, though they may not be publishable next year and may never be acceptable to scientific magazines of wide circulation, will continue to promote the still very necessary "rapid growth of knowledge" about tropical entomofaunas.

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BOOK REVIEW

BUTTERFLIES OF OREGON, by Ernst J. Dornfeld. 1980. Timber Press. Order from International Scholarly Book Services, Inc., Dept. B, 2130 Pacific Avenue, Forest Grove, Oregon 97116. Format: 8½ × 11″. 276 pp., 4 color plates, 48 halftone plates, 35 text halftones, 45 line drawings, 192 distribution maps. Cloth. Price $24.95 + 1.00 shipping. (The copy received for review was a paperback but no separate price was quoted.)

This book, which has been many years in preparation, is an extensive study of Oregon butterflies. It opens with an historical background of collectors and collecting in the state with an accompanying list of species described from Oregon localities. Then follow discussions of Oregon's physiography (illustrated) and associated butterfly distributions, butterfly biology, endangered and extinct butterflies, evolution, classification and nomenclature. The final sections of the introductory material treat collecting methods, rearing and photographing butterflies. These introductory sections occupy 36 pages and are well illustrated. The physiography section with its associated photographs should be invaluable to non-resident collectors planning a visit to Oregon.

The preliminary sections are followed by 81 pages that comprise the "Systematic Account." The families are ordered: Papilionidae, Pieridae, Danaidae, Satyridae, Nymphalidae, Riodinidae, Lycaenidae, Hesperiidae. One hundred and fifty-five species are discussed. Each species discussion is arranged in two columns of text with references to plate, figure and map numbers. Distinguishing characters of each species are clearly stated along with pertinent life history information. In many instances, literature references are included. Each family is introduced by a well-annotated prefatory statement.

The appendices include in order: color plates, halftone plates, maps, checklist, glossary of terms, index of butterfly names. The halftone plate legends reference each figure to the appropriate text page. The distribution maps are by county (counties not identified by name) with dots for each locality.

Generally speaking, the book is very well done and very thorough. For the most part, the taxonomic usage reflects current trends. The author has not accepted fully some recent revisionary work at the generic level. In these instances, he has used generic/subgeneric headings. Some examples are: *Pieris* (*Artogeia*), *Euphydryas* (*Occidryas*), *Lycaena* (*Epidemia*). This is a matter of personal preference and in no way detracts from the book. No new taxa are introduced, but some new combinations are

used such as *Callophrys sheridanii lemberti*. *Euphydryas colon* is treated as a sub-species of *E. chalcedona*. The trinomial *Incisalia fotis mossii* has been retained, rather than the form *I. mossii mossii* now accepted by many lepidopterists. If one accepts the taxonomic work of Higgins and Riley in Europe, then *Agriades aquilo podarce* should be listed as *A. glandon podarce*. *A. glandon* is the montane species, while *aquilo* occurs in arctic coastal regions. Some specialists consider the North American species as distinct from their European counterparts.

Genitalic sketches are included throughout the text, whenever such information is necessary, to assist in making positive identifications. The text descriptions always give sufficient information to assist in making differential diagnoses when two or more look-alike species are involved.

The color plates (photographs) are good, with 86 specimens and 85 species repre-sented in the first three plates. The fourth color plate illustrates a pair of Oregon's state insect, *Papilio oregonius*. These plates reflect a good balance of colorful butterflies (probably requested by the publisher), and ventral views to assist in identification of some difficult species. The halftone plates are excellent and collectors should have little difficulty in using them.

The book has so many positive features that the reviewer is reluctant to introduce any negative comments. There are, however, a few items that require passing comment. At first reading, some of the species headings appear inconsistent. When more than one subspecies is discussed, the heading includes only genus and species; when only one subspecies occurs in Oregon, the heading includes the complete trinomial.

Several items were noted in the section on *Colias*. It appears that this section was prepared toward the onset of the overall project and the associated literature references are not nearly so complete or current as in other sections of the book. The author appears reluctantly to treat *C. eurytheme* and *philodice* as separate species. There is no reference to the body of literature developed during the past decade that reflects the many ultraviolet light studies of *Colias*. Many authors have stated positively that *C. eurytheme*, *philodice* and the Old World *chrysotheme* are, in fact, distinct species based both upon ultraviolet reflectance from the wings and biological factors.

Dr. Dornfeld apparently recognizes only *Colias alexandra edwardsii* in Oregon, when there are actually two very distinct entities and some clinal forms. The rather striking population from the Ochoco Mts. in Crook Co. is not mentioned. The females are polymorphic and both sexes are distinct from *edwardsii*. Some collectors have confused this *alexandra* with *occidentalis*. Doubtful males can be separated easily by ultraviolet reflectance photography; *C. alexandra* produces a characteristic reflectance pattern, *C. occidentalis* produces no pattern. The females may pose some substantial identification problems. Plate I, f. 12 and Plate 6, f. 5c may represent *alexandra* and not *occidentalis* as stated.

No discussion appears of the quite local and isolated population of *Colias gigantea* that occurs in the Ochoco Mts. These butterflies are intermediate between nominate *gigantea* and *harroweri*.

Colias is a difficult genus and the items mentioned are perhaps minor, but for the sake of completeness, the reviewer would like to have seen this section expanded.

BUTTERFLIES OF OREGON contains a wealth of information and should be in the library of any collector who is interested in the butterfly fauna of western North Amer-ica. It is not just a state book since many of the butterflies mentioned have ranges into several states and Canada. The text is very readable and should appeal to professional and amateur alike. This book is comprehensive, well documented, and I recommend it highly.

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SUSCEPTIBILITY OF *PIERIS NAPI MICROSTRIATA* (PIERIDAE) TO *APANTELES GLOMERATUS* (HYMENOPTERA, BRACONIDAE)

The braconid wasp *Apanteles glomeratus* (L.) is probably the commonest parasitoid attacking *Pieris rapae* (L.) in North America, where it was apparently introduced in the 19th Century (Scudder, 1889, *Butterflies of E. U.S.*, Scudder, Cambridge, Mass.). Although Klots (1951, *Field Guide to the Butterflies*, Houghton Mifflin, Boston) suggested that the decline of *Pieris virginiensis* Edw. populations might be due to "the parasitic wasps that breed in great numbers in *rapae*," almost nothing is known of the interactions of this Palearctic parasitoid with the native pierid fauna. Most native pierids, like their crucifer hosts, are active in spring. In North America *A. glomeratus* is multivoltine, rare early in the season and commonest in autumn. We might thus predict a small impact on the native, vernal fauna. This is particularly true in California, where the Mediterranean climate enforces vernal uni- or bivoltinism and only two species of pierines (*P. protodice* Bdv. & LeC., *P rapae*) fly after June at low elevations. In Yolo Co. up to 70% of large collections of *rapae* larvae may be parasitized by *A. glomeratus* from September through November; parasitism of *P. protodice* rarely exceeds 10% at the same season (Shapiro, 1979, J. Res. Lepid., 17: 1–16, and unpublished data) but may reach 30% when populations are low.

In the Vaca Hills, Inner Coast Ranges, Solano Co., the following crucifer-feeding pierids occur in sympatry: *P. rapae*, *P. napi microstriata* Comstock, *P. sisymbrii* Bdv., *Anthocharis sara* Lucas, and *Euchloe ausonides* Lucas. Of these, *rapae* is multivoltine, *sisymbrii* strictly univoltine, and the others facultatively bivoltine (*ausonides* strongly, the others weakly). From 1972 through 1979 I collected and reared over 700 wild larvae, representing good samples of all of these species from the Vaca Hills, and reared *A. glomeratus* only from *P. rapae* and only after early May. Of the native species, *P. sisymbrii* has been found to harbor *A. glomeratus* at 1500 m in the Sierra Nevada.

In 1980 *A. glomeratus* was exceptionally common in spring. The frequency of *Apanteles* attack in wild larvae collected in the Vaca Hills in April was: *P. rapae*, 6/6; *P. n. microstriata*, 0/16; *A. sara*, 0/6; *E. ausonides*, 0/24. Some of the *ausonides* came from the same individual hosts as some of the *rapae*. There is a strong suggestion that *A. glomeratus* had access to, but discriminated against, the native vernal fauna in the Vacas in 1980.

Sato (1976, Appl. Ent. Zool., 11: 165–175) found that in Japan, *P. napi nesis* Fruhstorfer and *P. melete* Mén. were resistant to *A. glomeratus*, but *P. n. japonica* Shirôzu was not. S. R. Bowden has suggested (*in litt.*) that members of the *napi* complex in the northwest Pacific and California might be related; resistance to *Apanteles* would bear on this hypothesis. The *A. glomeratus* culture established from the 6 Vaca *rapae* was used to test the susceptibility of *P. n. microstriata* to attack. Lab-reared second-instar larvae from ova laid by a female from Lang Crossing, Nevada Co., 1400 m, on the Sierran west slope, were exposed to gravid female *A. glomeratus* and were seen to be stung repeatedly. The host plant was *Brassica kaber* (DC.) Wheeler. The culture was maintained at 25°C under continuous light.

Of the 8 larvae stung 9 May, one died in the 3rd and two in the 4th instars; one pupated and entered diapause; one pupated and eclosed normally 9 June; and three produced parasitoids in the normal manner, yielding 17, 21, and 24 wasps. The initial Vaca *rapae* had produced 17, 29, 23, 16, 19, and 38 wasps.

This quite uncontrolled experiment does not establish the relative attractiveness of *P. rapae* and *P. n. microstriata* as hosts. It merely demonstrates that there is no *absolute* barrier to attack by, and development of, *A. glomeratus* in the native species, and the apparent discrimination against it in the field must reflect behavioral or ecological factors.

Arthur M. Shapiro, *Department of Zoology, University of California, Davis, California 95616.*

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Contributions to the *Journal* may deal with any aspect of the collection and study of Lepidoptera. Contributors should prepare manuscripts according to the following instructions.

Abstract: A brief abstract should precede the text of all articles.

Text: Manuscripts should be submitted in *triplicate*, and must be typewritten, *entirely double-spaced*, employing wide margins, on one side only of white, 8½ × 11 inch paper. Titles should be explicit and descriptive of the article's content, including the family name of the subject, but must be kept as short as possible. The first mention of a plant or animal in the text should include the *full scientific name*, with *authors* of zoological names. Insect measurements should be given in *metric units*; times should be given in terms of the *24-hour clock* (e.g. 0930, not 9:30 AM). Underline only where *italics* are intended. References to footnotes should be numbered consecutively, and the footnotes typed on a separate sheet.

Literature Cited: References in the text of articles should be given as, Sheppard (1959) or (Sheppard 1959, 1961a, 1961b) and all must be listed alphabetically under the heading LITERATURE CITED, in the following format:

SHEPPARD, P. M. 1959. Natural selection and heredity. 2nd. ed. Hutchinson, London. 209 pp.

——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10: 165–216.

In the case of general notes, references should be given in the text as, Sheppard (1961, Adv. Genet. 10: 165–216) or (Sheppard 1961, Sym. R. Entomol. Soc. London 1: 23–30).

Illustrations: All photographs and drawings should be mounted on stiff, *white* backing, arranged in the desired format, allowing (with particular regard to lettering) for reduction to their final width (usually 4½ inches). Illustrations larger than 8½ × 11 inches are not acceptable and should be reduced photographically to that size or smaller. The author's name, figure numbers as cited in the text, and an indication of the article's title should be printed *on the back* of each mounted plate. Figures, both line drawings and halftones (photographs), should be numbered consecutively in Arabic numerals. The term "plate" should not be employed. *Figure legends* must be typewritten, double-spaced, *on a separate sheet* (not attached to the illustrations), headed EXPLANATION OF FIGURES, with a separate paragraph devoted to each page of illustrations.

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CONTENTS

JOURNAL

of the

LEPIDOPTERISTS' SOCIETY

13 May 1982

The object of the Lepidopterists' Society, which was formed in May, 1947 and formally constituted in December, 1950, is "to promote the science of lepidopterology in all its branches, ... to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

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Cover Illustration: Adult male *Anthocharis sara* Lucas (Pieridae) on inflorescence of fiddleneck (*Amsinckia intermedia* Fischer & Meyer, Boraginaceae). These butterflies occur in central Arizona during spring, often flying through small canyons and washes. Their larvae feed on a wide variety of mustards (Cruciferae). Original drawing by Dr. Rosser W. Garrison, Calle Iris UU18B, Rio Piedras, Puerto Rico 00926.

Journal of

The Lepidopterists' Society

FREQUENCIES OF THE MELANIC MORPH OF *BISTON COGNATARIA* (GEOMETRIDAE) IN A LOW-POLLUTION AREA OF PENNSYLVANIA FROM 1971 TO 1978

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ABSTRACT. The frequency of melanics in *Biston cognataria* was monitored for eight years in a low-pollution area near Klingerstown, Pennsylvania. A total of 3148 specimens was taken by UV light trap, on 528 nights; fewer than 1% were females. Over the long period a fairly stable equilibrium was maintained at about 52% melanics. There were only two statistically significant year-to-year deviations in melanic frequency—a rise in 1973 and a decline in 1978. No clear directional shift was evident. There was no significant difference in frequencies between the first and second annual generations. Fluctuations in abundance and in several climatic factors during this study period did not affect the melanic frequency.

Industrial melanism in many species of cryptic moths has been widely studied in Great Britain and some areas of the European continent (summarized by Kettlewell, 1961, 1973; Robinson, 1971). In North America the documentation is not yet extensive, but evidence of long-term increases and possibly decreases in frequency of melanic moths appears to be emerging (Kettlewell, 1957, 1958, 1961; Remington, 1958; Owen, 1961, 1962; Sargent, 1969, 1974), often in close relatives of the European species.

Kettlewell (1973) estimated that over 100 species in North America may prove to show melanic polymorphism. Owen (1962) listed 20 species of American Geometridae showing significant melanism, based on his rapid examination of museum collections. Sargent (1974) reported on six of these species he had followed in Massachusetts over a five-year period. In my current studies in central-eastern Pennsylvania, beginning in 1971, the nightly operation of a light trap for sampling *Biston cognataria* (Guenée) has also revealed abundant melanics of *Phigalia titea* (Cramer), *Ectropis crepuscularia* (Denis
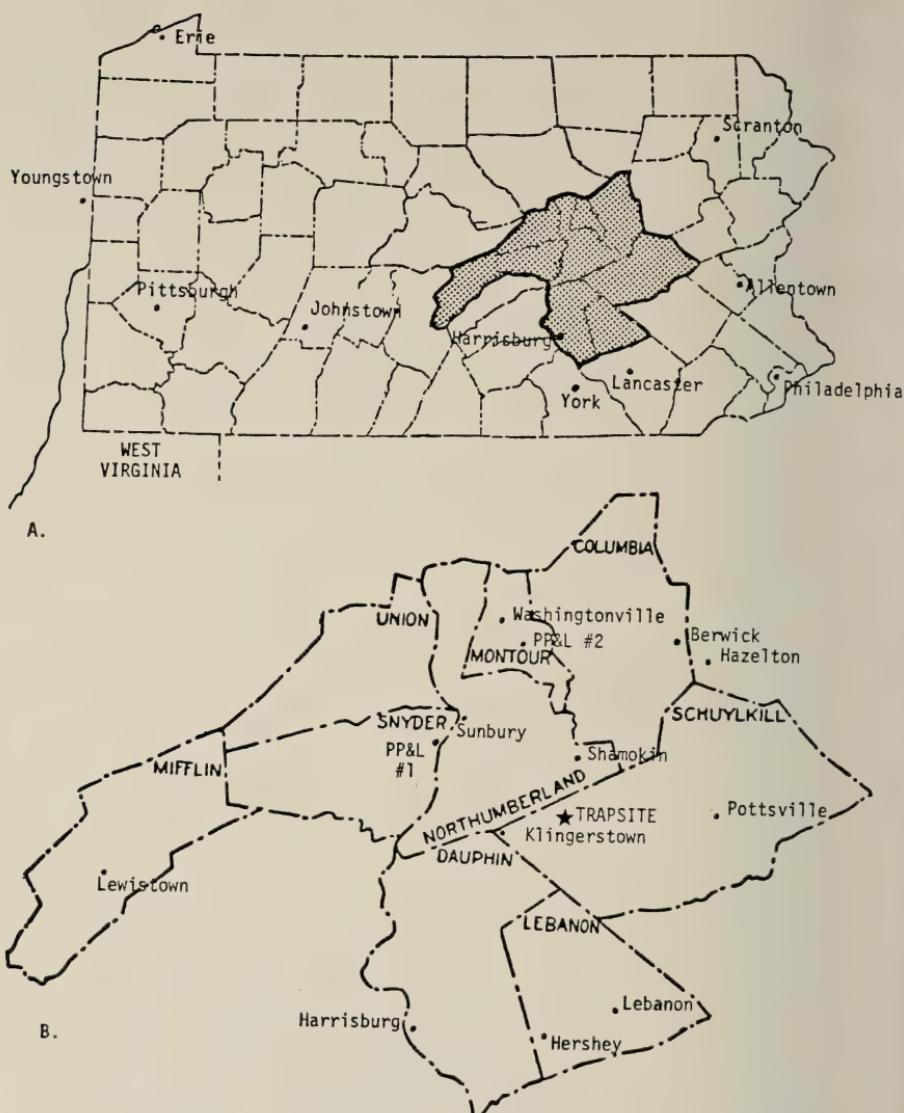
FIG. 1. (**A**) County map of Pennsylvania showing the location of the major industrial cities. Those west of the stippled area are potential sources of gaseous pollution critical to corticolous lichens and *Lycia* at the trapsite. (**B**) Counties surrounding the trapsite, with principal industrial areas capable of producing gaseous pollutants designated.

& Schiffermüller), *Epimecis hortaria* (Fabricius) and *Charadra deridens* (Guenée), and an occasional melanic of *Catocala ultronia* (Hübner).

The change in the flora of eastern North America, beginning with

the decline of the last major glaciation around 12,000 years b.p., with coniferous forests being extensively replaced by broad-leaved trees and high rainfall and humidity, probably provided excellent conditions for lichens to cover tree trunks. Lichens, however, are extremely sensitive to the gaseous pollution that results from industrialization in North America as in Europe (see, e.g., Kettlewell, 1973). Thus a reduction in the pale corticolous lichens, or their elimination in extremely polluted areas, plus blackening of tree trunks by soot accumulation, probably provided a new cryptic background for melanic phenes of bark-resting moths. Sargent (1974) suggested that another human activity, logging, selectively removed mature trees, such as white pine with lighter furrowed bark, causing a new prevalence of younger trees with darker smooth bark; this also would favor melanics. He further suggested that long before European colonization and industrialization, forest fires may have repeatedly blackened vast areas, making dark resting moths the most cryptic. All of these conditions favor melanic forms of corticolous Lepidoptera.

Biston cognataria is one of the most abundant geometrids exhibiting melanism in central-eastern Pennsylvania. Increases in the melanic form of this moth have been noted by many lepidopterists in the vicinity of highly industrialized areas (see, e.g., Owen, 1961, 1962; West, 1977).

Although the Palearctic *Biston* (*Biston* acvt) *betularia* L. may have been separated from *B. cognataria* for many thousands of years, hybrids between these species are at least partially fertile (Kettlewell, 1955, 1959; West, 1977), and they are morphologically very close and may prove to be the same biological species (see, e.g., Rindge, 1975). It is thus not surprising that melanism in *B. cognataria* appears to parallel that of *B. betularia* (e.g., Robinson, 1971; Kettlewell, 1973).

This paper reports eight years of recording the incidence of the melanic phene ("swettaria") of *B. cognataria* and the non-melanic phene in a relatively pollution-free environment. New potential sources of pollution are being built in the area, especially coal-burning power plants and an experimental coal gasification plant in Shamokin, and I intend to continue the sampling for several years to monitor melanic frequencies for comparisons with the pre-industrial period reported here.

SAMPLE SITE AND METHODS

The sampling area (see map, Fig. 1B) is an isolated tree-covered mountain and valley environment with small, cleared areas of pasture and field corn, 12 km northeast of Klingerstown, Schuylkill Co., Pennsylvania. This sampling area is 30 km southeast of Sunbury, Penn-

sylvania, location of a large coal-burning power plant; it is 55 air km north-northeast of Harrisburg and 37 air km west of Pottsville, the other nearest areas of major pollution. The nearest small city, Shamokin, 17 km to the northeast and at present not a major source of pollution, is separated by the heavily forested Mahanoy Mountains. Since the wind movement is primarily west to east, the nearest windward major polluter is Lewistown, 83 air km west. Several mountain ranges and the broad Juniata and Susquehanna river valleys probably influence air movement and cause significant reduction of pollutants prior to arrival of Lewistown air at the collecting area.

Among pollutants, it is interesting to note that the level of acid precipitation in Pennsylvania is one of the highest in the eastern United States (Likens et al., 1979), but the acid rain and snow have not eliminated the corticolous lichens that are usually considered the pivotal factor in tree-trunk color to which resting *Biston* are adapting (see, e.g., Kettlewell, 1973).

A tripod light trap with funnel opening about 1 m above the ground, with a 15-watt blacklite fluorescent tube as the ultraviolet source and with a cyanogas killing chamber, was operated nightly from 1 May to 15 September each year. The trap was emptied each day and all specimens of *Biston cognataria* and other potential industrial melanic species were saved, pinned, and later spread for study.

Daily recordings of minimum and maximum temperatures were made at the trap site. These, plus precipitation, cloud cover, fog and phases of moon are the subject of a separate paper on annual and seasonal abundance of *B. cognataria*, along with snow cover and depth, freezing periods and above-ground temperatures for the winters preceding each sample set.

Voltinism

The present study did establish that *Biston cognataria* in Pennsylvania is bivoltine, as two distinct generations were obvious when the sample numbers were large. The first generation normally emerges during the later part of May, peaks during mid-June, with a rapid decline by the second week of July. The second generation commonly emerges in late July, peaks during the third week of August, and rapidly declines during the first week of September. This conclusion is further supported by the lack of pupal diapause in the brood produced by a female taken 12 May 1973. All pupae of this latter brood hatched by mid-August of that year. Since the melanic frequency did not change between the early and late generations each year (see below), seasonal physical factors will not be examined closely in the present paper.

The Tree-Trunk Substrate

The normal resting place for *Biston* is on the trunks of trees, where, as expected for a palatable cryptic moth, they indeed blend with the background. As a tree-trunk rester, it is potentially vulnerable to visual predation by birds; thus, strong selection must exist for site selection behavior favoring crypsis (Tingergen, 1960; Kettlewell, 1973).

Although natural resting sites of *Biston cognataria* have not been extensively recorded, Kettlewell (1973, p. 108) stated for *B. betularia* in England that "both sexes spend the day at rest on the boughs and trunks of trees," and the same seems likely for *B. cognataria* in North America.

It is, therefore, of importance to note the tree types of the research area. The tree community near the trap consists of the following predominant species. Eight have pale trunks, *Quercus alba* L., *Acer rubrum* L., *A. pennsylvanicum* L., *Betula populifolia* Marsh., *Fraxinus lanceolata* Sarg., *Robinia pseudoacacia* L., *Juglans cinerea* L., and *Populus grandidentata* Michx. The common dark-barked species are *Quercus rubra* L., *Juglans nigra* L., *Cornus florida* L., *Pinus strobus* L., *P. virginiana* Mell., *Tsuga canadensis* L., *Prunus serotina* Ehrh., *Acer saccharinum* L., and *Tilia americana* L. Two intermediate-colored species, *Carya ovata* Koch and *Liriodendron tulipifera* L., provide a fairly suitable background color for both forms of the moth, depending on the part of the tree used for resting. Trunks are often lichen-covered at least on the northern side. With the rather uniform distribution over the area of different tree species presenting a range of black colors, suitable resting sites were readily accessible to both forms and moths could be so evenly dispersed that predator searches are minimally productive.

Melanic Frequency

A wide range of melanic frequencies of *Biston cognataria* have been reported in North America. In Livingston Co., Michigan, a highly industrialized area, samples from 1951 to 1961 were 87.0 to 93.0% melanic (Owen, 1961). In Leverett, Massachusetts, a non-industrialized area, samples for 1971 to 1974 ranged from 0 to 5.6% melanic (Sargent, 1974, 1976). These represent the recorded extremes for *Biston* melanism in North America.

Table 1 shows the distribution of melanic frequencies in the population samples taken in the present study in east-central Pennsylvania. During the eight-year study covering 1059 potential trapping nights, a total of 3148 *Biston* were taken on 528 nights. Less than 1% are females, perhaps due to the elevated position of the trap opening. The moths were grouped into 190 four-day samples for analysis. Data

TABLE 1. The numbers and percentages of melanic forms of *Biston cognataria* in each generation and for the season trapped near Klingerstown, Pennsylvania (1971–1978).

Year	Generation	Number melanic	Number non-melanic each brood	Percent of melanic each brood	Percent of melanics for season
1971	1	140	134	51.1	
	2	167	147	53.1	52.2
1972	1	126	114	52.5	
	2	214	215	49.9	50.8
1973	1	247	182	57.6	
	2	216	183	54.2	55.9
1974	1	51	55	48.1	
	2	91	75	54.8	52.2
1975	1	2	1	66.0	
	2	51	48	51.5	52.0
1976	1	40	32	55.5	
	2	76	71	51.7	52.9
1977	1	59	51	53.6	
	2	65	69	48.5	50.8
1978	1	22	35	38.6	
	2	82	87	48.5	46.1
Totals	1	687	604	53.2	
	2	962	895	51.8	
		1649	1499	52.4	

acquired from this site are more comprehensive than from sites previously reported and have been subjected to a wider range of tests.

In separating my melanic from non-melanic forms the breeding experiments with *B. betularia* by Clarke & Sheppard (1964) and Kettlewell (1963) were used as guidelines; those authors showed that incomplete dominance exists for melanics of that species. Modifiers quantitatively dilute the black pigment, creating a descending scale of phenotypic forms between the jet black ("carbonaria"), dark gray (most "insularia"), and the lightest ("typica"). Owen (1962) recognized similar forms in *B. cognataria* in North America and suggested the operation of a similar gene complex. However, more recently Clarke (1979) has noted the difficulty in distinguishing phenotypically the two dark forms "insularia" and "carbonaria" in *B. betularia*. Faced with the same assay problem with my trapped *cognataria*, I scored as "melanic" only the very darkest phenotypes. For guidance I was aided by a brood reared from a wild Pennsylvania female, all known to be homozygous for the recessive, non-melanic allele. These show the usual slight variations in the suffusion of black scales, not

related to the incompletely dominant allele for the full melanic, and helped me to score as "non-melanic" the moderately dark forms taken at the trap. Some of these dark individuals appear nearly black; however, the typical pattern of the non-melanic was visible beneath the heavy suffusion of black scales covering the wings and body of the moth. To establish a degree of uniformity in scoring the trap samples, only those moths whose color exceeded that of the darkest individuals in the reared brood were considered to be true melanics and were included in the melanic count. The number of the dark intermediate forms difficult to classify taken in the trap represented only 6.2% of the "melanic" population (some were present in both annual generations). Since the difficult individuals were so few, and the criteria were used equally for all years' samples, any errors in the phenotypic assay could not have influenced the results significantly.

From an examination of Table 1, two major questions can be answered: First—"Are there changes in melanic frequency from year to year?"; second—"Is there a shift in the frequency of melanics from the early, diapausing, generation to the summer non-diapausing generation?"; note that the early generation emerging from pupal diapause would have been subject to low winter and spring soil temperatures surrounding the pupae, and the summer generation would have developed under a more uniform and higher pupal temperature range, with moisture being the principal variant.

As the statistical analysis summarized below showed, there was no significant shift in frequency from the first to second generation each season. There were four years where the melanic frequency increased from 2.17%–9.93% in the second generation, over the first; three years the melanic frequency decreased by 2.61%–6.31% in the second generation. The small shifts do not appear to be environmental responses in Darwinian selection, as the largest difference during 1978 showed a rise in melanic frequency in the second generation of 9.93, following the most severe winter of the study and average summer temperatures, while the second largest rise, 6.69 in 1974 followed the mildest winter and an average summer; nor did the smallest negative shifts in the second generation follow any pattern of climatic variation.

For analysis within each generation, some four-nightly samples were pooled so that samples with 15 or more moths were obtained throughout, with most containing 25 or more. The significance of year-to-year and first-to-second generation variation in melanic frequencies was then examined via a two-way analysis of variance (ANOVA), on arcsine transformed data, using the methods of Sokal & Rohlf (1969; with correction for unequal subclass numbers, Steel & Torrie, 1960). Table 2 shows the ANOVA results over the entire span of years,

TABLE 2. Analysis of changes in melanic frequency by generations and years. Two-way ANOVA on arcsine transformed data as discussed in text. Year-year variation in melanic frequencies is highly significant, while generation-generation variation and year-generation interactions are not.

Source	df	SS	Ms	F	
A (years)	7	558.62	79.80	3.82	P < .001
B (generations)	1	6.49	6.49	.31	.75 > P > .50
A × B	7	199.74	28.53	1.37	.25 > P > .10
Within	75	1565.98	20.88		
Total	90	2349.74			

and for both generations per year. Highly significant variation among years is seen, but not between the two yearly generations. Yet Table 1 suggests that even the yearly frequencies are similar if the two most deviant from the 8-year mean (1973, 1978) are excluded. In order to test homogeneity of various yearly sets, several further tests were performed.

First, the most deviant frequencies relative to the 8-year mean were excluded—one by one—and the remaining sets analyzed for significant year to year variation in melanic frequency, again using ANOVA. The 1978 sample (lowest frequency) was omitted, and year-to-year variation was still found to be significant ($F_{6,68} = 2.61$, $.025 > P > .01$). Exclusion of the 1973 sample (highest frequency) also indicated significant remaining year-to-year variation ($F_{6,58} = 2.29$, $.05 > P > .025$). After omission of both 1973 and 1978, however, the year-to-year variance component fell far below significance ($F_{5,51} = 1.02$, $.50 > P > .25$). Both year-generation and generation-generation (early vs. late) interactions remained insignificant throughout ($.25 > P > .10$, or greater). Using a second, fundamentally similar approach, transforms of melanic frequencies were pooled among generations within years and these yearly samples searched for significance by a sum of squares simultaneous test procedure (SS-STP; see Gabriel, 1964). Here again, exclusion of both 1973 and 1978 produced a set of samples without significant differences (SS = 78.8, $.50 > P > .25$). Excluding only 1973 makes the remaining set just marginally homogeneous (SS = 237.5; $.10 > P > .05$), while excluding only 1978 shows higher heterogeneity (SS = 338.0, $P < .05$). A Student-Newman-Keuls analysis also returns similar sets of significantly different samples (.05 level). These latter two analyses (SS-STP, SNK) complement the ANOVA in showing that the years 1971, 1972, 1974, 1975, 1976, 1977 exhibit a homogeneous array of melanic frequencies, with 1973 and 1978 representing significant divergent frequencies.

These data show a fairly stable equilibrium between melanics and non-melanics, with occasional perturbations above and below the mean. No clear directional trend in melanic frequency is yet apparent when all eight years are examined together (Spearman rank correlation; R = 0.43, $p > .20$ two-tailed). After 1973, however, the yearly means suggest a gradual decrease in melanic frequency (R = 0.83, $p = .086$ two-tailed). The 1979, 1980 and 1981 sequels to the 1978 decrease will be of special interest. Continued sampling of *Biston cognataria* at this locality is underway and projected.

LITERATURE CITED

CLARKE, C. A. 1979. *Biston betularia*, obligate form *insularia* indistinguishable from form *carbonaria* (Geometridae). J. Lepid. Soc., 33:60–64.

———— & SHEPPARD, P. M. 1964. Genetic control of the melanic form *insularia* of the moth *Biston betularia* L. Nature, London, 202:215–216.

GABRIEL, K. R. 1964. A procedure for testing the homogeneity of all sets of means in analysis of variance. Biometrics, 20:459–477.

KETTLEWELL, H. BD. 1957. Industrial melanism in moths and its contributions to our knowledge of evolution. Proc. Roy. Inst. Gt. Brit., 36:164, 1–13.

———— 1958. A study of the frequencies of *Biston betularia* L. (Lep.) and its melanic forms in Britain. Heredity, London, 12:52–72.

———— 1961. The phenomenon of Industrial Melanism in Lepidoptera. Ann. Rev. Antomol., 6:245–262.

———— 1973. The Evolution of Melanism: The Study of a Recurring Necessity. Oxford: Clarendon. xxiv + 424 pp.

LIKENS, G. E., R. F. WRIGHT, J. N. GALLOWAY & T. J. BUTLER. 1979. Acid rain. Sci. Amer., 241(4):43–51.

OWEN, D. F. 1961. Industrial melanism in North American moths. Amer. Nat., 95:227–233.

———— 1962. The evolution of melanism in six species of North American geometrid moths. Ann. Ent. Soc. Amer., 55:695–703.

REMINGTON, C. L. 1958. Genetics of populations of Lepidoptera. Proc. 10th Int. Congr. Entomol., (1956) 2:787–805.

RINDGE, F. H. 1975. A revision of the New World Bistonini. Bull. Amer. Mus. Nat. Hist., 156:69–156.

ROBINSON, R. 1971. Lepidoptera Genetics. Oxford: Pergamon Press. 671 pp.

ROHLF, F. J. & R. R. SOKAL. 1969. Statistical Tables. San Francisco: W. H. Freeman and Co. 253 pp.

SARGENT, T. D. 1969. Background selections of the pale and melanic forms of the cryptic moth *Phigalia titea* (Cramer). Nature, London, 222:585–586.

———— 1974. Melanism in moths of Central Massachusetts (Noctuidae; Geometridae). J. Lepid. Soc., 28:145–152.

———— 1976. Legion of Night: The Underwing Moths. Amherst, Mass.: Univ. Mass. Press. 222 pp.

SOKAL, R. R. & F. J. ROHLF. 1969. Biometry. San Francisco: W. H. Freeman and Co. 776 pp.

STEEL, R. G. D. & J. H. TORRIE. 1960. Principles and Procedures in Statistics. New York: McGraw-Hill. 481 pp.

TINBERGEN, L. 1960. Natural control of insects in pine woods. (1) Factors influencing intensity of predation by song birds. Archs. néerl. zool., 13:264–343.

TREAT, A. E. 1979. *Biston cognataria*: Frequency of melanic males in Tryingham, Mass. 1958–1977. J. Lepid. Soc., 33:148–149.

WEST, DAVID A. 1977. Melanism in *Biston* (Lepidoptera: Geometridae) in the Rural Central Appalachians. Heredity, 39(1):75–81.

THE EFFECT OF FEMALE MATING FREQUENCY ON EGG FERTILITY IN THE BLACK SWALLOWTAIL, *PAPILIO POLYXENES ASTERIUS* (PAPILIONIDAE)

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ABSTRACT. Most black swallowtail females mate more than once to replace a sperm supply that has deteriorated with time, although some do so to replace a deficient spermatophore. Fecundities and oviposition rates correlated significantly with weights of females at emergence. Courtship flights were brief ($\bar{x}$ = 42.4 sec) and copulations averaged 44.8 min. Average mating frequency increased as females became older, with an overall mean of 1.30. Although there was no relationship between the number of eggs oviposited and the fertility of those eggs, the average fertility of eggs decreased significantly 10 days after the female mated. Older monogamous females had lower fertilities than young monogamous or older multiple-mated females. The short lifespan of most butterflies results in a mating mode of one.

Multiple mating has been detected in all subfamilies of butterflies and in several skippers (Burns, 1968; Pliske, 1973; Ehrlich & Ehrlich, 1978) and appears to be the norm in many species. Sperm precedence, reviewed by Parker (1970), clearly indicates the advantage of multiple mating for males. In most Lepidoptera, the last male to mate with a female sires the majority of her subsequent offspring (Clarke & Sheppard, 1962; Ae, 1962; Labine, 1966). The adaptive advantage of multiple mating for females that absorb the spermatophore (Taylor, 1967) may be the acquisition of nutrients such as nitrogen (Boggs & Gilbert, 1979). However, an advantage for females where the spermatophore persists other than nutrient acquisition (Boggs & Watt, 1981) has not been demonstrated.

This study was designed to evaluate three of the most common hypotheses for multiple mating in female butterflies. Females may mate more often than they need to rather than refuse or evade a persistent male (Alcock et al., 1977). There may be too few spermatozoa in one insemination to fertilize all of the eggs that a female will lay (Ehrlich & Ehrlich, 1978). Sperm may deteriorate with age and must be replaced with a fresh supply (Labine, 1966). Females of the black swallowtail, *Papilio polyxenes asterius* Stoll were studied, since preliminary dissections indicated that spermatophores persisted throughout the lives of females, and a portion of field-collected females carried more than one spermatophore. In evaluating these hypotheses, I determined the ability of females to reject copulation attempts and estimated the costs involved in additional copulations. The fertility

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of eggs was determined relative to the ovipositional sequence and to the period since mating. I also compared the hatchabilities of eggs from fresh and worn females that had mated once or more than once.

MATERIALS AND METHODS

Field observations of courtships and copulations were made near Ithaca, New York, often using marked individuals. Females dissected to determine mating frequency were collected from field sites at different times during each brood. Most females were rated for wing condition when collected (Lederhouse, 1978). The females in the experimental groups were reared in the laboratory from eggs laid by field-collected females. Newly-emerged females were hand-paired with males that were at least two days old (Clarke & Sheppard, 1956). Females were paired once with males copulating for the first time. Some males were paired on successive days to additional females not in the experimental group. All pairing was done at 22°C in a controlled chamber.

To determine fecundity and fertility, females were placed in individual cloth-covered cages (0.3 m × 0.3 m × 0.6 m) with potted cultivated carrot plants. The cages were in a bioclimatic chamber with a 16 h light and 8 h dark photoperiod. Daytime temperature was 22°C and the night time temperature was 15°C. Each female was fed twice daily with a 50% honey-water solution, and her eggs were counted daily. When about 50 eggs had accumulated on a plant, it was removed from the cage and replaced with a fresh plant. The plants were kept in the bioclimatic chamber until all eggs had hatched or until 10 days had elapsed since the last egg had hatched. Larvae were counted and collected daily. Ten days after the last larva hatched, unhatched eggs were counted, and their stage of development was recorded. The experiment continued for each female until she died. Each female was dissected to determine the presence of a spermatophore. Females that lacked a spermatophore, oviposited for less than 5 days, or laid fewer than 50 eggs were excluded from the analysis of fecundity.

In *Papilio polyxenes,* a brown ring appears in the upper half of the yellow egg as development proceeds (Ae, 1979). When the embryo is fully formed, the egg turns black. Thus, eggs that showed no signs of development were classified as infertile. Eggs that developed partially but failed to hatch were classified as inviable. Egg fertility and hatchability were calculated only for those females that laid 25 or more eggs of which some hatched.

RESULTS

The total number of eggs laid (fecundity) correlated significantly with the initial weight of black swallowtail females after emergence
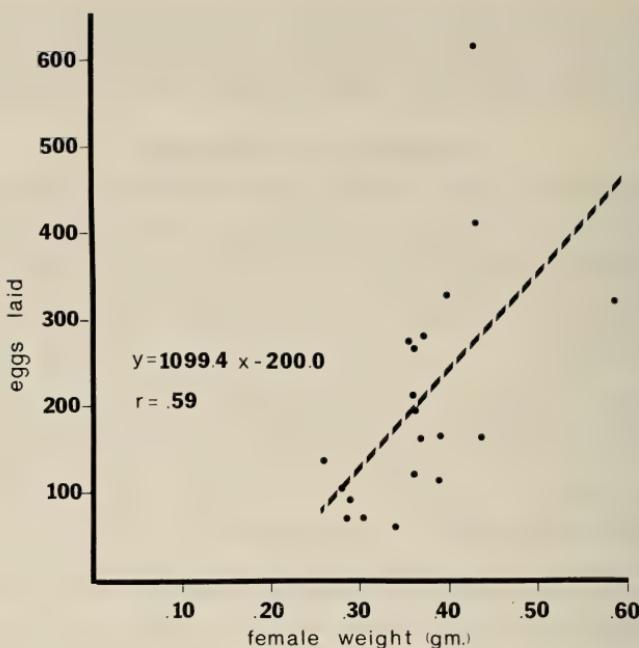
FIG. 1. The relationship between female weight and egg production under laboratory conditions.

(Fig. 1). The mean period between mating and the start of oviposition for 33 females was 3.5 ± 2.5 days. Freshly emerged females had few mature ova (12.9 ± 3.4, n = 7) when dissected during the first day after emergence. Females that were not paired until their second or third adult day had a shorter period between mating and oviposition. The mean number of eggs laid by females meeting the sampling criteria was 205.9 ± 136.9 under the chamber conditions. The oviposition rate correlated significantly with female weight (Fig. 2). The total number of eggs also correlated significantly with the length of the oviposition period (Fig. 3). However, the relationship between the length of the oviposition period and female weight was not significant ($r = 0.25$, P > 0.05).

Courtship flights that terminated in copulation were brief (Table 1). The female flew a short distance (19.8 ± 18.4 m, n = 16) after the male started to court. If receptive, she would land on a perch, and the male would land nearby and initiate copulation. The female had to land for copulation to take place. However, if the female was not receptive, she would attempt to evade the courting male. This resulting in mating-refusal flights of significantly longer duration (Table 1, Mann-Whitney U Test, P < 0.001). Usually the female would fly
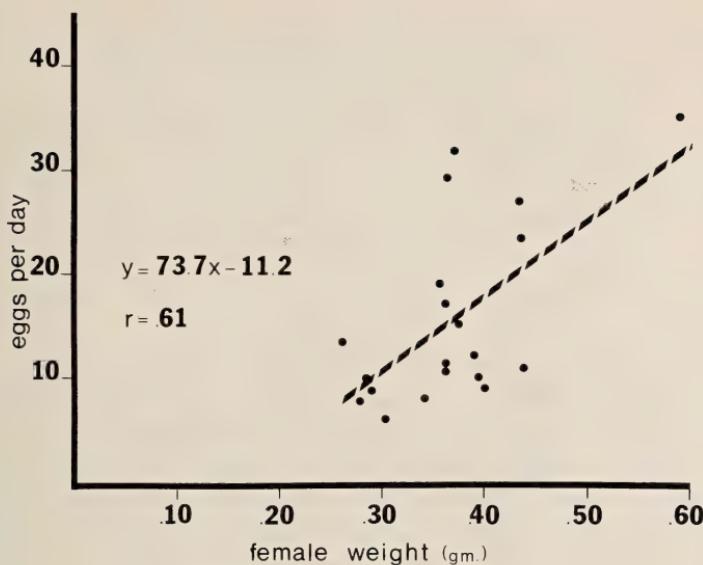
Fig. 2. The relationship between female weight and oviposition rate under laboratory conditions.

high into the air (>10 m) and dive rapidly if followed. This pattern was repeated until the male gave up or was evaded.

The mean duration for copulations in the field was significantly shorter than the mean of hand-paired copulations in the laboratory (Table 1, Mann-Whitney U Test, P < 0.01). Males that mated frequently had much longer copulation durations. The second pairings within 24 h of laboratory males were significantly longer (Mann-Whitney U Test, P < 0.04). Likewise, the second copulations of field males that mated twice on the same day were longer than the average duration of field copulations (Mann-Whitney U Test, P < 0.01).

The reliability of spermatophore counts in estimating frequency of mating of black swallowtail females was confirmed by dissecting 84 females that had been hand-paired a single time. Of these, 79 contained one spermatophore, and the remaining five had none. Single matings never resulted in the passage of more than one spermatophore (Sims, 1979). Females that lived longer under laboratory conditions (>35 days) than field females could be expected to live contained spermatophores that were easily detected. The spermatophore shells were still thick and tough, yet the spermatophore itself was usually collapsed. Although some pairings did not result in the passage of a spermatophore, counts did accurately measure the frequency
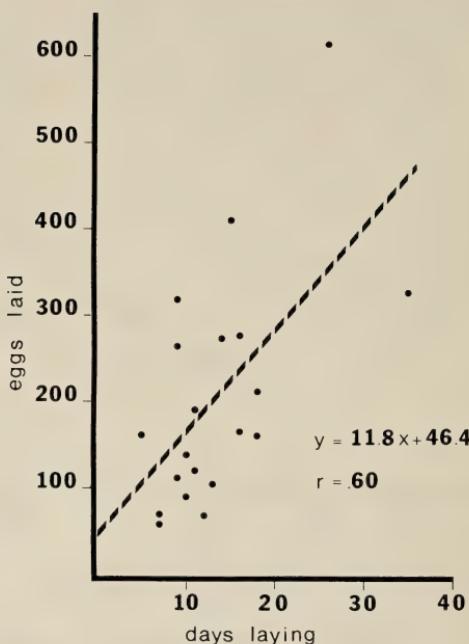
FIG. 3. The relationship between laying period and egg production under labora-
tory conditions.

of insemination. Although no pair-bond is formed, females that have
mated once have been termed monogamous (Wiklund, 1977b). Fe-
males that mate more than once would therefore be polyandrous.

The average width for 26 *Papilio polyxenes* spermatophores from
single hand-pairings in this study was 1.92 ± 0.32 mm, which is al-
most identical to values reported by Sims (1979) for the closely related
P. zelicaon Lucas. Using Sims' method of calculation and assuming
the same sperm density, an average value of 800,000 sperm per cop-
ulation was calculated for 2–5 day old males. Even if storage is low
(20%, Lefevre & Jonsson, 1962), there would be about 160,000 sperm
to fertilize no more than 600 to 800 eggs or about 200 to 1. However,
the first copulation of some females results in few or no viable sperm
being transferred. Some females containing small spermatophores
laid no fertile eggs.

Females that had been collected from the field for a variety of pur-
poses were pooled to determine an average mating frequency. The
mean number of spermatophores contained by 171 females was
1.30 ± 0.54. Only 2.3% of the females were virgin, and three individ-

TABLE 1. The durations of courtships and copulations.

Interaction	n	Mean	S.D.
Courtship leading to copulation	33	42.4 sec	40.5
Mating refusal flight	22	99.8 sec	74.4
Copulation (field)	21	44.8 min	12.3
Copulation (laboratory)	22	51.3 min	8.6
Second copulation on same day (field)	3	256.2 min	93.1
Second copulation within 24 h (laboratory)	7	78.5 min	30.0

uals had mated three times (Table 2). First and second brood females yielded nearly identical mean frequencies (Table 3). The mean of third brood females was somewhat lower but not significantly different from those of the first and second broods. Means of yearly samples from the second brood were quite consistent for three years (Table 3).

Females in condition classes showing greater wear had significantly higher mean numbers of spermatophores (Table 2). When fresh or slightly worn, females contained two spermatophores, usually one or both were smaller than average. In most cases, the position of the smaller spermatophore indicated that it had been deposited first.

To determine whether older females mated again to prevent a drop in fertility related to the number of eggs already laid or to the period of time since the last mating, the influence of the expected correlation between these two factors had to be removed. Since the rate of oviposition was positively correlated with adult weight, these alternative factors were distinguished by determining the fertility and hatchability of eggs laid by females of different initial weights that had been hand-paired once. Sequential samples of about 50 eggs were ranked according to fertility and hatchability for each female. The results for 10 females, each with four samples, and for five females with five samples were nearly random (Friedman two-way analysis of

TABLE 2. Female mating frequencies related to wing condition. z and P values are for a one-tailed Mann-Whitney U Test.

Condition class	Number of spermatophores					z	P
	0	1	2	3	Mean		
Fresh	4	36	1	0	0.93	3.63	<0.001
Slightly worn	0	37	13	0	1.26	1.88	<0.031
Intermediate	0	16	14	0	1.47	2.16	<0.016
Very worn	0	6	12	3	1.86		
Undetermined	0	20	9	0	1.31		
Total	4	115	49	3	1.30		

Table 3. Female mating frequencies related to brood and year.

| Brood | Year | | Percent of females in each spermatophore class | | | | |
		n	0	1	2	3	Mean
First		41	2.4	68.3	24.4	4.9	1.32
Second		109	2.8	63.3	33.0	0.9	1.32
Third		21	0.0	85.7	14.3	0.0	1.14
Second	1974	22	4.5	59.1	36.4	0.0	1.32
Second	1975	42	2.4	61.9	35.7	0.0	1.33
Second	1976	45	2.2	66.7	28.9	2.2	1.31

variance, Siegel, 1956). Fertility and hatchability were independent of the number of eggs that had been laid previously.

Although the fertility and egg hatchability of singly-paired females did not decrease with the number of eggs they laid, they did decrease with the time since mating. The egg hatchabilities of 16 of 18 individuals (88.9%) were fairly constant through the first 10 days after mating. Samples from 11 females that had oviposited until at least 15 days after mating were divided into those laid less than 8 days, those laid 8 to 14 days, and those laid more than 14 days after mating. When these categories were ranked by fertility and hatchability, a significant decrease was related to the length of the period since mating in both (Table 4, Friedman two-way analysis of variance, χ^2_r for fertility = 7.8, df = 2, P < 0.05, χ^2_r for hatchability = 8.9, P < 0.05). However, the percent of fertile but inviable eggs showed no relationship with the duration since mating. One female was hand-paired a second time 16 days after her first mating. She showed an increase in hatchability of her eggs and a decrease in the percent of infertile eggs.

The relationship between the period between mating and oviposition and the fertility of eggs was further investigated with field-

Table 4. The fertility and viability of eggs laid during the first, second, and third weeks after mating by females hand-paired once. The top value is the mean and the lower value is the standard deviation (n = 11).

| Egg class | Days laid after mating | | |
	1–7	8–14	15+
Infertile	8.4	17.3	31.8
	8.3	16.5	32.8
Inviable	10.7	12.9	9.5
	8.5	8.6	9.5
Hatched	80.9	69.8	58.7
	11.8	19.7	32.1

collected females. Since the exact period between mating and oviposition could not be determined, it was estimated from the condition of the female at the time of capture. The hatchability of eggs laid by 23 females was recorded. The females were grouped by condition and the number of spermatophores they contained. Slightly worn and intermediate classes were pooled. Fresh monogamous females had significantly higher egg hatchabilities than slightly worn and intermediate females that had mated once (98.8 ± 1.0% vs. 81.7 ± 23.9%, $U = 8$, $P < 0.05$). Worn females that had mated more than once had significantly higher egg hatchabilities (98.1 ± 1.8%) than monogamous females of slightly worn and intermediate condition ($U = 13$, $P < 0.05$). However, fresh monogamous females did not differ from worn polyandrous females. The egg hatchabilities of all field-captured females with one spermatophore did not differ from singly-paired laboratory females (Mann-Whitney U Test, $z = 1.41$, $P > 0.15$). The egg hatchabilities of all field females combined were significantly higher than those of laboratory females mated a single time ($z = 2.31$, $P < 0.05$). Mating an additional time restored the hatchability of eggs of old females to the level of a fresh, newly-mated female.

DISCUSSION

Females of many butterfly species can reject male advances by signals (Wago, 1977; Wiklund, 1977b), postures (Shapiro, 1970; Scott, 1973; Suzuki et al., 1977), and evasive flights (Stride, 1958; Rutowski, 1978). The evasive flights of black swallowtail females seem quite effective in this regard. Since the duration of a mating-refusal flight is very short compared to that of a copulation, it is unlikely that a female would mate rather than refuse or evade a courting male. This conclusion is reinforced by the increase in copulation duration of males that have mated frequently. Thus in a species with effective mating-refusal behaviors such as *P. polyxenes*, a female controls how frequently she mates, as long as males are available.

P. polyxenes females mate for the first time soon after emergence. Virgin females were rarely captured as in other species (Shields, 1967; Burns, 1968). Each was collected on the mating territory of a male (Lederhouse, 1982). Released virgin females flew preferentially to male territories as reported for *P. zelicaon* (Shields, 1967). It is likely that most females mate by the end of their first adult day.

The mean mating frequency of *P. polyxenes* was very consistent from brood to brood and from year to year (Table 3, Sims, 1979). This consistency contrasts with considerable variation in the density of males on mating areas (Lederhouse, 1978). The male density during the second brood of 1975 was more than twice that of both first and

second broods of the other years. Such uniformity in mating frequency would not be expected if females were mating more than they needed to. Burns (1968) reported an inverse relationship between population density and mating frequency for several species of skippers. However, positive correlations have been reported for a pyralid moth (Goodwin & Madsen, 1964) and a gelechiid (Graham et al., 1965). In a hilltop territorial mating system, the availability of male mates may be relatively independent of the absolute species density. Females would have similar opportunities to mate as long as the main territories were occupied. The trend of a lower mean mating frequency in third brood females may result from shorter average longevities of the females, rather than a scarcity of males since no virgins were collected. Thus, mating frequency may be independent of density in a hilltopping species.

A normal first copulation provides ample sperm to fertilize all the eggs that a female is likely to lay (Labine, 1966; Suzuki, 1978; Sims, 1979). Therefore, it is not surprising that there is no decline in fertility related to the number of eggs a female has laid previously. However, spermatophores with a low sperm count may result from young males or males that have mated frequently prior to the mating in question (Sims, 1979). These spermatophores are considerably smaller than average. Sugawara (1979) has demonstrated the importance of spermatophore size in controlling female receptivity. In *Pieris rapae crucivora* Boisduval, a mated female remained receptive unless her bursa copulatrix was stretched by a volume one half the size of the average spermatophore or greater. This agrees with the observation that fresh or slightly worn females that have mated twice frequently have a small first spermatophore. Thus a portion of polyandrous females mate again to replace a deficient initial spermatophore.

An increase in mean mating frequency with female age is well documented (Pliske, 1973; Ehrlich & Ehrlich, 1978; Sims, 1979; Suzuki, 1979). David & Gardiner (1961) report a refractory period between effective matings for *Pieris brassicae* (L.) females of six to nine days under laboratory conditions. *Pieris rapae crucivora* females mate for a second time at about 8 days of age under field conditions (Suzuki, 1979). Nearly three-quarters of the very worn females in this study had mated more than once. Although one normal copulation transfers abundant sperm, the sperm of the black swallowtail deteriorates with time. Thus, a high percentage of eggs laid late in a female's life may fail to develop if she has mated only once. An additional mating restores fertility levels, probably as a result of sperm precedence. Although female butterflies may not be able to determine directly the quality of stored sperm, the collapse of the spermatophore with time

may serve as an indirect measure. Once it has collapsed sufficiently, the sexual receptivity of the mated female is restored (Sugawara, 1979).

The cost to a female that mates an additional time may be quite low. The actual copulation consumes less than one hour. The cost only becomes considerable if the female must move a great distance from oviposition habitat to a mating area and back again (Wiklund, 1977a). Although there is a delay between mating and oviposition in newly emerged females, there is none for females after an additional mating. The benefit of mating again can be substantial. The mean egg hatchability of older condition class females that had mated once was 17.1% lower than fresh monogamous females. Their mean egg hatchability was also 16.4% lower than females in similar condition that had mated more than once. Similarly, the mean egg hatchability of all females in the laboratory dropped 15.8% between the first 10 days and after the fifteenth day. Since several of these females dropped to below 50% fertility, the benefit of an additional mating must surely outweigh its cost.

The prevalence of monogamous females in studies that have counted spermatophores has been interpreted as indicating that monogamy is the most adaptive female mating strategy (Wiklund, 1977b). The rationale is that the time saved by mating only once can be used for locating host plants and ovipositing, thus maximizing reproductive output. However, this is true only if high fertility is maintained throughout the lifetime of the female. A mating mode of one is a result of the short lifespan of most butterflies (Scott, 1974). The majority of females in most species die before a second mating becomes advantageous. If the mortality rate of *P. polyxenes* females is similar to that of males (Rawlins & Lederhouse, 1978), less than 35% of the females would be expected to live more than the 10 days of uniform fertility. Actually 30.4% of the sampled females had mated more than once. Evidently, most females that live long enough to make an additional mating advantageous, in fact do mate again.

LITERATURE CITED

AE, S. A. 1962. Some problems in hybrids between *Papilio bianor* and *P. maackii*. Academia (Nazan Univ.), 33:21–28.
——— 1979. The phylogeny of some *Papilio* species based on interspecific hybridization data. Syst. Entomol., 4:1–16.

Alcock, J., G. C. Eickwort & K. R. Eickwort. 1977. The reproductive behavior of *Anthidium maculosum* (Hymenoptera: Megachilidae) and the evolutionary significance of multiple copulations by females. Behav. Ecol. Sociobiol., 2:385–396.

Boggs, C. L. & L. E. Gilbert. 1979. Male contribution to egg production in butterflies: Evidence for transfer of nutrients at mating. Science, 206:83–84.

Boggs, C. L. & W. B. Watt. 1981. Population structure of Pierid butterflies. IV. Genetic and physiological investment in offspring by male *Colias*. Oecologia, 50:320–324.

Burns, J. M. 1968. Mating frequency in natural populations of skippers and butterflies as determined by spermatophore counts. Proc. Nat. Acad. Sci. U.S.A., 61:852–859.

Clarke, C. A. & P. M. Sheppard. 1956. Hand-pairing of butterflies. Lepid. News, 10:47–53.

——— 1962. Offspring from double matings in swallowtail butterflies. The Entomologist, 95:199–203.

David, W. A. L. & B. O. C. Gardiner. 1961. The mating behaviour of *Pieris brassicae* (L.) in a laboratory culture. Bull. Ent. Res., 52:263–280.

Ehrlich, A. H. & P. R. Ehrlich. 1978. Reproductive strategies in the butterflies: I. Mating frequency, plugging, and egg number. J. Kansas Entomol. Soc., 51:666–697.

Goodwin, J. A. & H. F. Madsen. 1964. Mating and oviposition behavior of the navel orangeworm, *Paramyelois transitella* (Walker). Hilgardia, 35:507–525.

Graham, H. M., P. A. Glick, M. T. Ouye & D. F. Martin. 1965. Mating frequency of female pink bollworms collected from light traps. Ann. Entomol. Soc. Am., 58:595–596.

Labine, P. A. 1966. The population biology of the butterfly, *Euphydryas editha*. IV. Sperm precedence—a preliminary report. Evolution, 20:580–586.

Lederhouse, R. C. 1978. Territorial behavior and reproductive ecology of the black swallowtail butterfly, *Papilio polyxenes asterius* Stoll. Unpublished Ph.D. thesis, Cornell University. 155 pp.

——— 1982. Territorial defense and lek behavior of the black swallowtail butterfly, *Papilio polyxenes*. Behav. Ecol. Sociobiol., in press.

Lefevre, G., Jr. & U. B. Jonsson. 1962. Sperm transfer, storage, displacement, and utilization in *Drosophilia melanogaster*. Genetics, 47:1719–1736.

Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev., 45:525–567.

Pliske, T. E. 1973. Factors determining mating frequencies in some New World butterflies and skippers. Ann. Entomol. Soc. Amer., 66:164–169.

Rawlins, J. E. & R. C. Lederhouse. 1978. The influence of environmental factors on roosting in the black swallowtail, *Papilio polyxenes asterius* Stoll (Papilionidae). J. Lepid. Soc., 32:145–159.

Rutowski, R. L. 1978. The form and function of ascending flights in *Colias* butterflies. Behav. Ecol. Sociobiol., 3:163–172.

Scott, J. A. 1973. Mating of butterflies. J. Res. Lepid., 11:99–127.

——— 1974. Lifespan of butterflies. J. Res. Lepid., 12:225–230.

Shapiro, A. M. 1970. The role of sexual behavior in density-related dispersal of pierid butterflies. Am. Nat., 104:367–372.

Shields, O. 1967. Hilltopping. J. Res. Lepid., 6:69–178.

Siegel, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York. xvii + 312 pp.

Sims, S. R. 1979. Aspects of mating frequency and reproductive maturity in *Papilio zelicaon*. Amer. Midl. Natur., 102:36–50.

Stride, G. O. 1958. Further studies on the courtship behavior of African mimetic butterflies. Anim. Behav., 6:224–230.

Sugawara, T. 1979. Stretch reception in the bursa copulatrix of the butterfly, *Pieris rapae crucivora*, and its role in behaviour. J. Comp. Physiol. A, 130:191–199.

Suzuki, Y. 1978. Adult longevity and reproductive potential of the small cabbage white, *Pieris rapae crucivora* Boisduval (Lepidoptera: Pieridae). Appl. Ent. Zool., 13:312–313.

——— 1979. Mating frequency in females of the small cabbage white, *Pieris rapae crucivora* Boisduval (Lepidopterea:Pieridae). Kontyu, 47:335–339.

———, A. NAKANISHI, H. SHIMA, O. YATA & T. SAIGUSA. 1977. Mating behavior of four Japanese species of the genus *Pieris* (Lepidoptera, Pieridae). Kontyu, 45:300–313.

TAYLOR, O. R., JR. 1967. Relationship of multiple mating to fertility in *Atteva punctella* (Lepidoptera:Yponomeutidae). Ann. Entomol. Soc. Am., 60:583–590.

WAGO, H. 1977. Studies on the mating behaviour of the pale grass blue, *Zizeeria maha argia* (Lepidoptera, Lycaenidae). 2. Recognition of the proper mate by the male. Kontyu, 45:92–96.

WIKLUND, C. 1977a. Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapis* (Lepidoptera). Oikos, 28:56–68.

——— 1977b. Courtship behaviour in relation to female monogamy in *Leptidea sinapis* (Lepidoptera). Oikos, 29:275–283.

A NEW *CYDIA* (LEPIDOPTERA: TORTRICIDAE) FROM FLORIDA AND CUBA

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ABSTRACT. *Cydia largo* Heppner, new species, is described from Florida and Cuba.

The following description of a new *Cydia* (formerly *Laspeyresia*) concerns a species known for several decades but only recently collected in numbers. The first specimens were sent from Cuba to Washington in 1933. Thereafter another group of specimens was sent from Homestead and Tampa in 1944, then another group from Key West in 1945. Curators at the Smithsonian Institution noted that the species was new but it was not described. From 1973–1975 a number of additional specimens were collected on Key Largo and other areas, prompting this description.

Cydia largo, new species

Size. 3.0–4.0 mm forewing length.

Head. Buff, with buff-white frons; labial palpus tan and gray, with interior side white; antenna buff-gray.

Thorax. Buff; venter buff-white; legs buff-tan with fuscous on tibiae and tarsal segments. *Forewing:* dark fuscous ground color irrorated with buff, with more extensive buff area in central basal area; mid-wing line of darker fuscous from anal margin angled toward apex; costal margin with 6–7 black fuscous streaks bordered and merging into dark orange, angled toward tornus, with white spots between streaks along costal margin; mid-apical circular area buff, with 4 black spots in basal half and semi-circle of lustrous silver in distal half of buff circle; silvery area at tornus; ventral side lustrous dark fuscous; fringe dark fuscous. *Hindwing:* uniform dark fuscous; ventral side lustrous fuscous; fringe dark fuscous.

Abdomen. Fuscous; venter buff-white. *Male genitalia:* tegumen a simple band; un-

FIGS. 1–2. *Cydia largo* Heppner, new species, Florida (paratypes): **1**, ♂; **2**, ♀.
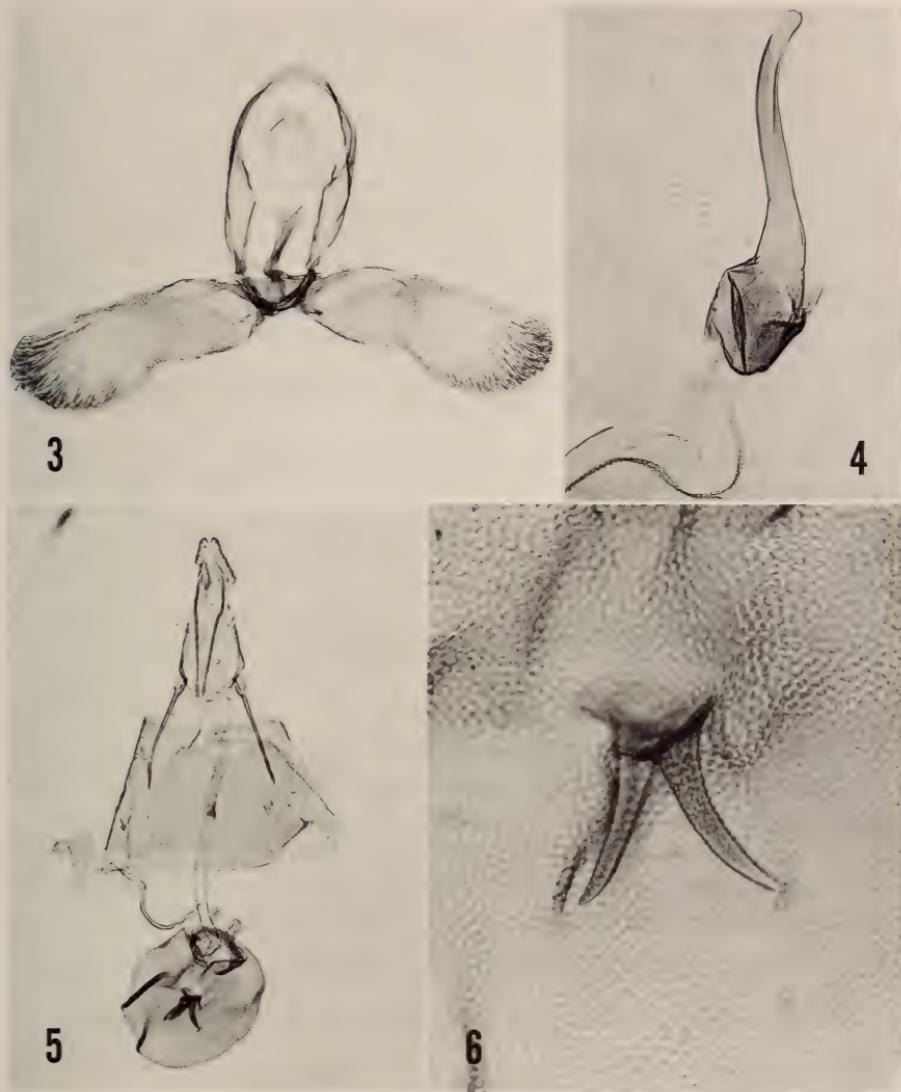
FIGS. 3–6. *Cydia largo* Heppner, new species, Florida: **3,** holotype ♂ genitalia; **4,** holotype ♂ aedeagus (enlarged); **5,** paratype ♀ genitalia; **6,** paratype ♀ signa (enlarged).

cus and gnathos absent; vinculum reduced; anellus an angled, narrow spatulate form; valva simple and elongate, rounded at apex with numerous stout inwardly directed setae, with a slight narrowing of the valva midway and then to base; aedeagus elongate with bulbous base and narrow, curved distal end; no cornuti evident. *Female genitalia:* ovipositor with setaceous papilla anales, of average length; apophyses subequal; ostium simple, membranous; ductus bursae narrow, elongate, unsclerotized; corpus bursa ovate, with 2 large thorn-like signa on opposite sides of the bursa and an almost united ring at junction with ductus bursa.

Types. *Holotype* ♂: 15 mi. NE Key Largo City, Key Largo Key, Monroe Co., FLOR-

IDA, 16 Jun 1974, J. B. Heppner (USNM type No. 76752). Genitalia slide USNM 77849. *Paratypes:* (31 ♂♂, 58 ♀♀) FLORIDA.—ALACHUA Co.: Gainesville, 15–22 Sep 1956 (4 ♂♂), ex *Acacia* sp., H. V. Weems, Jr. (FSCA). DADE Co.: Homestead, 26 May 1944 (1 ♂, 1 ♀), Jun 1944 (3 ♂♂, 10 ♀♀) ex *Lysiloma bahamensis* (USNM): 1 mi. W. Royal Palm, Everglades National Park, 25 Apr 1975 (1 ♀), J. B. Heppner (JBH); Long Pine Key, Everglades National Park, 26 Apr 1975 (1 ♀), 28 Apr 1975 (2 ♀♀), 30 Apr 1975 (5 ♀♀), J. B. Heppner (JBH). HILLSBOROUGH Co.: Tampa, 17 Jun 1944 (1 ♀), 20 Jun 1944 (2 ♂♂), ex *Acacia* sp. (USNM); Tampa, 21 Jun 1944 (1 ♀♀), ex *Sambucus canadensis* (USNM). MONROE Co.: 15 mi. NE. Key Largo City, Key Largo Key, 16 Jun 1974 (10 ♂♂, 21 ♀♀), J. B. Heppner (JBH); Key West, 31 Mar 1945 (1 ♂), 4 Apr 1945 (1 ♂, 1 ♀), 6 Apr 1945 (2 ♂♂, 1 ♀), 7 Apr 1945 (1 ♀), 10 Apr 1945 (1 ♂), ex "*Vachiella insularis*," (USNM); 2 mi. N. Tavernier, Key Largo, 17 Jun 1974 (2 ♂♂, 5 ♀♀), 20 Jun 1973 (2 ♂♂, 1 ♀), J. B. Heppner (JBH); 1 mi. SW. Islamorada, Upper Matecumbe Key, 23 Jun 1974 (1 ♂, 6 ♀♀), J. B. Heppner (JBH); Key Largo, 14 Jul 1967 (1 ♂), S. Kemp (CPK).

Paratypes will be distributed to the Florida State Collection of Arthropods, Gainesville (FSCA); British Museum (Natural History), London, England; and University of California, Berkeley.

Additional specimens: Cuba: Santiago de las Vegas, 20 Feb 1933 (1 ♀), 21 Feb 1933 (1 ♀), 24 Feb 1933 (1 ♂), 26 Feb 1933 (1 ♀), ex: *Inga dulcis,* A. Otero (USNM).

Hosts. *Acacia pinetorum* (Small) Hermann (="*Vachiella insularis*"); *Pithecellobium dulce* (Roxburg) Bentham (=*Inga dulcis* Willdenow); *Lysiloma latisiliqua* (Linnaeus) Bentham (=*Lysiloma bahamensis* Bentham) (Fabaceae). One specimen from Tampa is recorded as reared from *Sambucus* (Caprifoliaceae) but this may be erroneous (perhaps a pupation site).

Distribution. Cuba and southern Florida. (The Gainesville record may refer to a rearing from an ornamental plant outside the natural range of the moth.)

REMARKS

Dark specimens of *Goditha bumeliana* Heinrich, *Ricula maculana* (Fernald), and *Larisa subsolana* Miller have a superficial resemblance to *Cydia largo,* but the genitalia of the new species will serve to distinguish them. It is not evident which *Cydia* may be most closely related to *C. largo.* The Cuban specimens are not treated as paratypes but nonetheless show no significant differences in maculation or genital characters from the Florida specimens. Whether this species is of Cuban origin and introduced into Florida or whether it is native to Florida with further distribution in the Caribbean is not known.

ACKNOWLEDGMENTS

ARTIFICIAL DIETS AND CONTINUOUS REARING METHODS FOR THE SULFUR BUTTERFLIES *COLIAS EURYTHEME* AND *C. PHILODICE* (PIERIDAE)

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ABSTRACT. Two artificial diets, one based on alfalfa and the other on lima beans, were used to rear *Colias eurytheme* and *C. philodice* in the laboratory. Preparation of the diets and rearing methods are described. *C. eurytheme* had a higher survivorship on both diets and proved to be the easier species to maintain in long term culture. Despite slightly lower survival of both species on the lima bean diet, it seems to be the more advantageous of the two diets because of ease of preparation and lower cost.

The development of artificial diets and culturing techniques for rearing large numbers of Lepidopterous insects has proliferated over the last fifteen years and produced a large body of literature establishing diets for over 250 species (Singh, 1977). The use of artificial diets has several advantages: primarily it makes possible year-round rearing of large numbers of individuals independently of host plant resources; by following proper procedures, it is possible to raise many individuals in a small space with a minimum risk of loss to disease; additionally, experimentation, transport, and storage are also greatly enhanced with the use of artificial diets. Singh (1977) provides a thorough review of the advantages of rearing insects on artificial diets.

Two artificial diets and culturing methods which can be used for the laboratory rearing of two closely related sulfur butterflies, *Colias eurytheme* Boisduval and *C. philodice* Godart, are reported here. Due to its ubiquity, abundance, and many distinctive characteristics, *Colias* is an intensely studied genus with work ongoing concerning its genetics, behavior, physiology and ecology. Easy laboratory rearing of *Colias* on an artificial diet can greatly facilitate investigations involving this group.

REARING PROCEDURE

Laboratory cultures of *C. eurytheme* and *C. philodice* were started by placing, individually, young females captured in the wild (which are nearly always mated) in small oviposition chambers. The chamber consisted of two parts: a small round or square pint-size container filled with water and vermiculite in which sprigs of fresh alfalfa (*Med-*

icago sativa Linnaeus), vetch seedlings (*Vicia villosa* Roth), or plugs of white dutch clover (*Trifolium repens* Linnaeus) were placed; and a clear acetate cylinder about 3.5 inches in diameter and 6–7 inches in height with a one-inch wide strip of screen stapled around both ends. A petri dish lid served as a top for the chamber. The chamber was designed to permit air flow but prevent the female from clinging to the sides.

Maximum oviposition was obtained by placing the chambers containing single *Colias* females under fluorescent or incandescent lights. Egg laying usually started within 24 hours and often continued for 7–10 days. Leaves containing eggs were collected from the host plants every 48 hours and placed in a petri dish containing a moistened piece of paper towel. If eggs were not immediately placed in a food cup, they were stored in a refrigerator at 5–10°C. Eggs could be kept in this way with no detectable loss in viability for one week. A decrease in hatchability and larval viability was frequently noted when eggs were refrigerated for longer periods. Females were set up on new sprigs of the host plant every 48 hours and eggs were collected until the female died, except during the first generation fecundity test with *philodice*, which was based on the first three days of oviposition. Females were fed on 1:4 honey to water solution once each day. Fecundity varied greatly under these conditions, but it was not unusual to obtain 500 eggs from a single female.

Colias are plagued by polyhedral virus and other diseases. In an attempt to control trans-ovariole transmission of virus and other pathogens, eggs were surface decontaminated. Bits of leaves with eggs attached were placed in envelopes made from filter paper and immersed in a dilute solution of sodium hypochlorite (Clorox), consisting of 1 ml Clorox, 99 ml water and one drop of detergent, for 10 minutes and then immediately transferred to 100 ml rinse of tap water for another 10 minutes. The envelopes were then placed on filter paper to facilitate removal of excess water from around the eggs.

Eggs (5–20) were placed in 1.0 oz plastic cups containing about 0.25 oz of diet. Since formaldehyde in the preparation can kill the eggs, they were placed on the paper tab lids of the cups; these were then stored upside down until the larvae completed the first instar. These procedures also minimized exposure of the diet to mold spores and reduced the chance that eggs or young larvae would drown in condensation which occasionally accumulated on the surface of the diet. After the first instar, cups were turned on their sides to allow excess moisture to escape. This retarded the growth of mold.

Larvae were reared on the diet in an environmental chamber which

was maintained at elevated temperatures of 30–35°C and at room temperatures. A 16 hour light : 8 hour dark photoperiod was provided under both conditions. The relative humidity was usually 50–60%.

At room temperature eggs hatched in about 72 hours and larvae pupated in 2½ to 3 weeks. The pupal stage lasted 5 to 7 days, for a total egg to adult interval of 28 days. More information concerning developmental rates is contained in the following section.

Larvae were transferred to new cups of diet in 1½ to 2 weeks. This was necessary because of desiccation of the medium. At this time, no more than five larvae were placed in each cup to ensure food availability and to prevent crowding. Cups were kept on their sides to give the larvae access to diet, to provide a suitable surface on the sides of the cup for pupation and to allow excess moisture to escape.

Once larvae had pupated and the pupae had hardened for at least 24 hours, they were removed from the cups and placed in eclosion chambers. These consisted simply of a piece of plastic window screen rolled and stapled into a cylinder with petri dishes serving as top and bottom. The bottom of each chamber was covered by a thin layer of plaster of paris which was moistened to maintain high humidity. Paper towelling was placed over the plaster to provide a rough surface for adults to grip when eclosing. Usually, pupae were allowed to complete development at room temperature; however, we found that development could be halted with refrigeration at 5–10°C for three weeks with a minimum mortality or loss of vigor.

Newly eclosed adults were given at least an hour for their wings to harden before placing them in a mating cage positioned under a bank of 10, 1500 ma Daylight fluorescent bulbs. We used a cage 4½ × 5′ × 6′, with the top covered with clear mylar plastic and with sides consisting of white sheeting or plastic screen. Two to three hundred individuals could be maintained in this cage at one time. Smaller mating cages have also proven successful (Watt, pers. comm.). Synthetic household sponges saturated with honey water were placed in aluminum pans suspended in the cage daily as a food source for the active adults. The time of day and the number of matings were controlled by turning on the light bank over the cage. The greatest number of matings were obtained when females less than two days old were placed in the cage with 2–4 day old males. Copulations lasted 45 to 75 minutes; so, by monitoring the cage every 30 minutes while the light was on, it was possible to collect all the mating pairs. Females were selected from among the mating pairs (depending on the needs of our experiments) and set up for oviposition. Because of inbreeding depression, we avoided breeding from brother-sister matings or from other crosses among closely related individuals.

If vetch (*Vicia villosa*) or white clover (*Trifolium repens*) is substi-

tuted for alfalfa as the oviposition substrate, a laboratory culture of *Colias* can be maintained year-round with no need for any outdoor resources. Vetch is easily grown indoors and is used readily for oviposition by *C. eurytheme* and *C. philodice*. Vetch has been used by Watt and his students as a year-round host plant; however, extreme vigilance must be maintained to control diseases, and it is sometimes necessary to scrub the entire room with disinfectants if a continuous culture is being maintained (Watt, pers. comm.).

DIET PREPARATION

The alfalfa diet is a modified version of that developed by C. M. Ignoffo (1963) for the cabbage looper, *Trichoplusia ni* (Hübner) (Noctuidae); and was made up in groups which were combined at the time of preparation. The composition of the groups was as follows:

Alfalfa Diet

	Ingredient	Amount
Group 1	agar	40.0 g
	hot distilled water for dissolving agar	1600.0 ml
Group 2	distilled water	300.0 ml
	cholesterol	0.6 mg
	inositol	0.3 g
	choline chloride	2.0 g
	methyl *p*-hydroxybenzoate	3.0 g
	sorbic acid	3.0 g
	sucrose	35.0 g
	fructose	35.0 g
	wheat germ	70.0 g
	vitamin-free caseine	70.0 g
	dried chopped alfalfa	20.0 g
	biological salt mixture (Wesson modification)	20.0 g
	beta-sitosterol	1.0 g
	safflower oil (55% linoleic acid)	7.5 ml
	linolenic acid	7.5 ml
	40% formaldehyde	4.0 ml
	10% KOH	10.0 ml
Group 3	ascorbic acid	6.0 g
	distilled water to dissolve ascorbic acid	30.0 ml
	vitamin mix	30.0 ml

The vitamin mix was composed of the following:

distilled water	200.0 ml
nicotinic acid	200.0 mg
calcium pantothenate	200.0 mg
riboflavin	100.0 mg
thiamine HCl	50.0 mg
pyridoxine HCl	50.0 mg
folic acid	50.0 mg
biotin	20.0 mg
vitamin B_{12}	2.0 mg

The diet was prepared in the following manner: The components of Group 2 were added together and thoroughly mixed in a blender. Group 2 was then added to Group 1 after the agar was dissolved in the 1600 ml of hot water. This mixture was thoroughly stirred, and when it had cooled to below 60.0°C, Group 3 was added and again thoroughly stirred. The hot diet was then dispensed quickly into the 1 oz styrene cups, filling each cup approximately ⅓ full with about 8.5 ml (9.0 g) of the mixture. The cups were fitted with lids and stored in a refrigerator. This recipe yielded about 225 cups of diet. The growth of bacteria and fungi on the diet was controlled by the anti-microbial mixture consisting of methyl p-hydroxybenzoate, sorbic acid, and formaldehyde, which constituted .35% of the combined diet. The alfalfa served as a feeding stimulant as well as a source of nutrients.

Bean Diet

The second diet is very similar to the modified bean diet established by Burton (1969) for the corn ear worm, *Helothis zea* (Bodie) (Noctuidae). This diet was also made up in separate groups which were subsequently combined. Its constituents were the following:

	Ingredient	Amount
Group 1	agar	35.0 g
	hot distilled water for dissolving agar	700.0 ml
Group 2	wheat germ (not toasted)	100 g
	brewers yeast	64 g
	ascorbic acid	7 g
	sorbic acid	2 g
	methyl p-hydroxybenzoate	4 g
	10% formaldehyde	16 ml
Group 3	lima beans (soaked overnight)	200 g
	distilled water	200 ml

The preparation of the bean diet was as follows: Lima beans were soaked in water for 12 to 24 hours, and then they and the rest of the Group 2 ingredients were homogenized and mixed thoroughly in a blender. Group 2 was then added to Group 1, after the agar became completely dissolved, and thoroughly mixed in 700 ml of hot distilled water. This recipe yielded about 250 cups of diet. The diet contains a 1.1% anti-microbial mixture made up of methyl p-hydroxybenzoate, sorbic acid, and formaldehyde.

RESULTS

Colias philodice usually takes 1–3 days less to complete development from egg to adult on the diets than does *C. eurytheme*. Devel-

TABLE 1. Survivorship fecundity and mating fitness of *C. eurytheme* and *C. philodice* reared on artifical diets. Ranges are given in parentheses.

	Alfalfa diet*		Bean diet	
	eurytheme	*philodice*†	*eurytheme*	*philodice*
First generation survivorship (per brood)	x̄ = 30.8% (8–72%) n = 17	x̄ = 25.4% (4–68%) n = 16	x̄ = 50.0% (27.5–80%) n = 15	x̄ = 37.3% (13.8–48.6%) n = 8
First generation Males mating fitness (per brood)	x̄ = 31.7% (0–100%) n = 57	**	x̄ = 27.0% (0.0(1)–70.8%) n = 15	x̄ = 6.7% (0.0(4)–24.5%) n = 8
Females	x̄ = 66.4% (0–100%) n = 50	**	x̄ = 45.8% (12.0–50.0%) n = 15	x̄ = 8.7% (0.0(2)–27.8%) n = 8
First generation fecundity (per female)	x̄ = 292.1 (110–455) n = 9	x̄ = 129.3 (14–314) n = 23	x̄ = 99.6 (61–140) n = 7	x̄ = 74.0 (30–120) n = 9
Second generation survivorship (per brood)	x̄ = 66.1% (3–94%) n = 8	x̄ = 25.6% (4–54%) n = 12	x̄ = 22.8% (4.0–60.0%) n = 6	x̄ = 17.4% (0.00(1)–46.7%) n = 7
Fecundity of wild females (per female)	x̄ = 268.3 (59–458) n = 19	x̄ = 185.4 (15–314) n = 17		

* Survivorhsip for individuals reared on the alfalfa diet was recorded from egg-pupa, while those individuals reared on the bean diet were scored as adults (i.e., survivorship from egg to adult). Survivorship to the adult stage was usually 10–20% lower than that recorded through pupation.
† 1st generation fecundity for *C. philodice* was based on 3 days of oviposition for individuals reared on the alfalfa diet.
** Not recorded.

opmental rates were highly dependent on the temperature at which larvae and pupae were maintained. At room temperature *C. eurytheme* took 18–21 days to pupate, and adult eclosion followed in about 5–7 days. When reared at higher temperatures (30–35°C), pupation occurred in about 14–16 days. Thus, at room temperature the generation length for *C. eurytheme* is approximately 24–28 days and at 30–35°C, it is reduced to 21–22 days. By using refrigeration to "hold" eggs and pupae, we were able to synchronize and delay generations.

Some pertinent parameters indicative of diet suitability for laboratory rearing of *C. eurytheme* and *C. philodice* are summarized in Table 1.

Survivorship on the alfalfa diet varied greatly. Initially, survivorship of *C. eurytheme* was high (x̄ = 70%, N = 8 broods); large individuals emerged which mated readily and produced large egg clutches. In subsequent tests on different batches of diet, survivorship was lower, averaging 31% for *C. eurytheme* and 25% for *C. philodice* (Table 1). The latter results were more representative. While second

generation survivorship, fecundity and mating fitness were moderately high for the alfalfa diet, the substantial variance in overall survivorship of individuals on this diet led us to adopt the bean diet for use in our laboratory.

First generation survivorship is quite good on the bean diet, but again there is a difference between *C. eurytheme* and *C. philodice*, with lower survivorship for *C. philodice* (50.5 vs. 37.3%). While second generation survivorship shows a sharp decline for both *C. eurytheme* and *C. philodice*, this decline levels off substantially for subsequent generations (data not shown here).

A comparison of the two diets shows that, while the alfalfa diet is higher in fecundity, mating fitness and second generation survivorship, it is substantially lower in first generation survivorship. The difference in first generation survivorship is actually greater than shown in Table 1, since survivorship on the alfalfa diet was measured to the pupal stage, and usually, only 80–90% of the those reaching this stage become adults. In practice it was found that the greater number of first generation adults obtained with the bean diet was more important in maintaining the cultures than the differences between the diets in fecundity, mating fitness and second generation survivorship.

In *C. eurytheme*, the survivorship and mating viabilities of lab generations stayed high enough to maintain a continuous lab culture for 22 months. *C. philodice* presents greater culturing difficulties since it has lower first generation survivorship and mating viability, which then becomes even lower in the second generation. Because of this, it is necessary to add wild stock to a *C. philodice* culture whenever possible. Adding wild stock is desirable for both species to minimize the inbreeding which is an inevitable consequence of laboratory rearing.

Larvae reared on the diet were generally bluish when compared to larvae reared on natural hosts. The difference is evidently due to a lack of carotenoids in the diet (Rothschild, 1978).

DISCUSSION

In general, the bean diet is preferable to the alfalfa diet for the laboratory rearing of *C. eurytheme* and *C. philodice*. The data indicate that first generation survivorship is greater for individuals raised on the bean diet. However, fecundity, fertility, and mating fitness are greater with the alfalfa diet.

The primary difficulty with the alfalfa diet resides in the quality of the dried alfalfa. The alfalfa we used was obtained directly from commercial alfalfa drying plants. It seemed to vary greatly in its ability to

stimulate feeding, possibly because of the varieties of alfalfa, time of year of harvest, or contamination of fields by weed species which could contain feeding deterrents. It is also possible that some of our alfalfa sources contained natural or synthetic additives which were toxic to developing larvae. Another problem is that the alfalfa diet contains a large number of more or less purified sources of proteins, lipids, carbohydrates and vitamins, which must all retain their individual qualities or the quality of the diet is reduced. Additionally, the alfalfa diet is more expensive because of the large number of costly components it requires. In contrast, the bean diet utilizes mostly natural plant derivatives (beans and wheat germ) and yeast, which can be stored for a longer time without deterioration. Finally, because the bean diet is composed of fewer components, it can be prepared more quickly. We routinely prepared an entire batch of bean diet (about 250 cups) in 1–2 hours; whereas, it usually took 2–3 hours to prepare a similar quantity of the alfalfa diet.

Dehydration of the medium is a problem with both diets. The water content must be high enough to prevent desiccation of early instars and permit easy consumption. Larvae which have been raised on a diet with low moisture content often have difficulty emerging from the pupal case and many crippled adults are the result. Transferring larvae to new cups when the diet has become dehydrated and maintaining high humidity in the rearing chamber does much to eliminate this problem. Spraying pupae lightly with water several times a day often reduces adult eclosion problems.

Generally, *C. eurytheme* utilized both diets more successfully than *C. philodice*. We have no explanation for this, other than to speculate that there is some minor nutritional deficiency which resulted in lower *C. philodice* survivorship and viability. Another problem with *C. philodice* involved its low frequency of mating, which may in part have been due to an alteration in the male pheromones used in courtship. One of us (J.W.G.) has found that *C. philodice* males produce substantially smaller amounts of the three esters unique to this species when reared on the diet. *C. eurytheme* was not similarly affected (Grula et al., 1980).

Neither diet is complete, and since it is likely that survivorship, viability and fecundity are greater on natural hosts, both could be substantially improved. Nevertheless, both the alfalfa and bean diets have proven highly successful for mass rearing *C. eurytheme* and *C. philodice*. The alfalfa diet was used to raise large enough numbers of *C. eurytheme* and *C. philodice* to establish the inheritance of ultraviolet reflectance patterns characteristic of the dorsal wing surface of male *C. eurytheme* and *C. philodice* (Silberglied & Taylor, 1973).

The bean diet has been used to determine the genetic basis of male *C. eurytheme* and *C. philodice* pheromone production (Grula & Taylor, 1980) and inheritance of responses to those pheromones by females (Grula & Taylor, 1980).

Finally, we wish to point out that the bean diet has proven to be successful on a trial basis for rearing several other *Colias* species, including *C. alexandra* Edwards and *C. meadii* Edwards, and also the small pierid *Nathalis iole* Boisduval. We suspect that the bean diet, as formulated in this paper, with slight modifications, probably could be used for a wide variety of legume and composite-feeding butterflies. Its general use by a large number of noctuid moth species has already been demonstrated (Shorey & Hale, 1965).

LITERATURE CITED

BURTON, R. L. 1969. Mass rearing of the corn earworm in the laboratory. U.S. Dept. Agric. ARS Series 33–134, 8 pp.

IGNOFFO, C. M. 1963. A successful technique for mass-rearing cabbage loopers on a semisynthetic diet. Ann. Entomol. Soc. Am., 56:178–182.

GRULA, J. G., J. McCHESNEY & O. R. TAYLOR, JR. 1980. Aphrodisiac pheromones of sulfur butterflies, *Colias eurytheme* and *C. philodice*. J. Chem. Ecol., 6:241–256.

——— & O. R. TAYLOR, JR. 1979. Inheritance of pheromone production in the sulfur butterflies, *Colias eurytheme* and *C. philodice*. Heredity, 42:359–371.

——— 1980. The effect of X-chromosome inheritance on mate-selection behavior in the sulfur butterflies, *Colias eurytheme* and *C. philodice*. Evolution, 34(4):688–695.

ROTHSCHILD, M. 1978. Carotenoids in the evolution of signals: Experiments with insects (1974–1976), *in* Biochemical Aspects of Plant and Animal Coevolution, J. B. Harbourne, ed., Academic Press, N.Y. pp. 259–295.

SHOREY, H. H. & R. L. HALE. 1965. Mass-rearing of the larvae of nine noctuid species on a simple artificial medium. J. Econ. Ent., 58:522–524.

SILBERGLIED, R. E. & O. R. TAYLOR. 1973. Ultraviolet differences between the sulfur butterflies *Colias eurytheme* and *C. philodice*, and a possible isolating mechanism. Nature, 241(5389):406–408.

SINGH, P. 1977. Artificial Diets for Insects, Mites, and Spiders. IFI/Plenum, New York.

DESCRIPTION OF THE MATURE LARVA AND NOTES ON *HOLOCHROA DISSOCIARIA* (HULST) (GEOMETRIDAE: ENNOMINAE)[1]

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ABSTRACT. The mature larva of *Holochroa d. dissociaria* is described, with illustrations and photographs included. Notes on the life history are given, and related genera discussed.

Holochroa dissociaria (Hulst) (Figs. 13–14) inhabits the mountainous regions of the southwestern United States. The nominate subspecies occurs in Arizona and Colorado. Subspecies *varia* Rindge is known from New Mexico and western Texas. Three Mexican species also are recognized (Rindge, 1961, 1971).

Holochroa belongs to the Nacophorini, a new world tribe of 21 genera (Rindge, 1971; Ferguson, 1982). Rindge (1974) divided the tribe into a compact nominate group and a diverse nonnominate group. Of the four genera in the nominate group, *Nacophora* is more specialized and *Betulodes* and *Thyrinteina* more primitive than *Holochroa* on the basis of adult characters, but *Holochroa* is considered to be the most distantly related of these genera (Rindge, 1961). In the Nacophorini, only the larvae of *Nacophora*, *Ceratonyx* and *Aethaloida* have previously been studied.

MATERIALS AND METHODS

Nine mature larvae were examined. These were reared on juniper from single females collected at the following localities in Arizona: Walnut Canyon 6500', 6⅓ mi, ESE of Flagstaff, Coconino Co., July 16, 1965, R. W. Poole, five specimens on *Juniperus* spp.; Onion Saddle 7600', Chiricahua Mtns., Cochise Co., July 16, 1967, J. G. Franclemont, four specimens on *Juniperus pachyplaea* Torr.

Descriptions and drawings are based on these specimens. A Wild M-5 microscope and drawing tube attachment were used in making the illustrations. The larval photograph was taken by Dr. J. G. Franclemont, Department of Entomology, Cornell University. Adult photography and larval illustrations were done by the author. Measurements are based on the average of the available specimens.
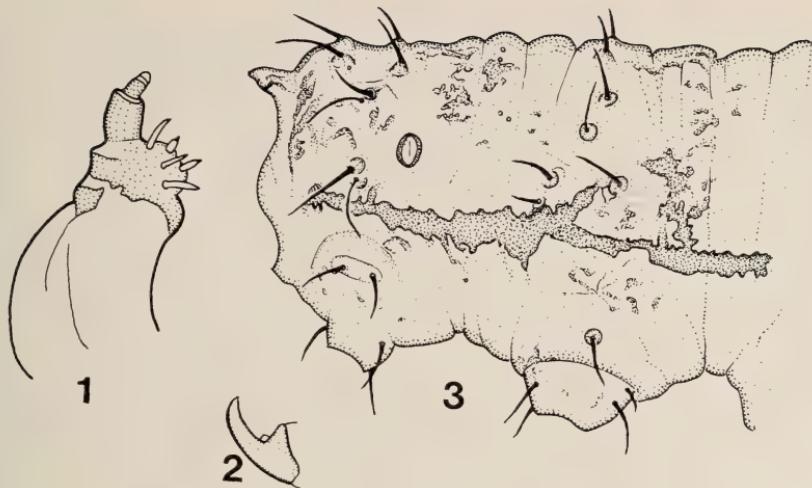
FIGS. 1–4. Larva of *H. dissociaria*. **1,** dorsal view of maxilla, 60×; **2,** thoracic leg claw, 60×; **3,** lateral view of pro- and mesothorax, 30×; **4,** lateral view of abdominal segments 6–10, 30×.

DESCRIPTION OF MATURE LARVAE

Head. Height, 2.7 mm; width, 2.5 mm; color mainly gray above ocelli due to compounded areas of epidermal pigment, cuticle otherwise light brown, with dorsal cream areas of prothorax extending onto top of head, prominent dark sclerotization on collar, about ocelli, in stripe through seta A2 and as a few irregular, small patches (Fig. 8); cuticle rugose and coarsely granular; shape strongly bifid (Fig. 9); ocellus 1 largest, 4
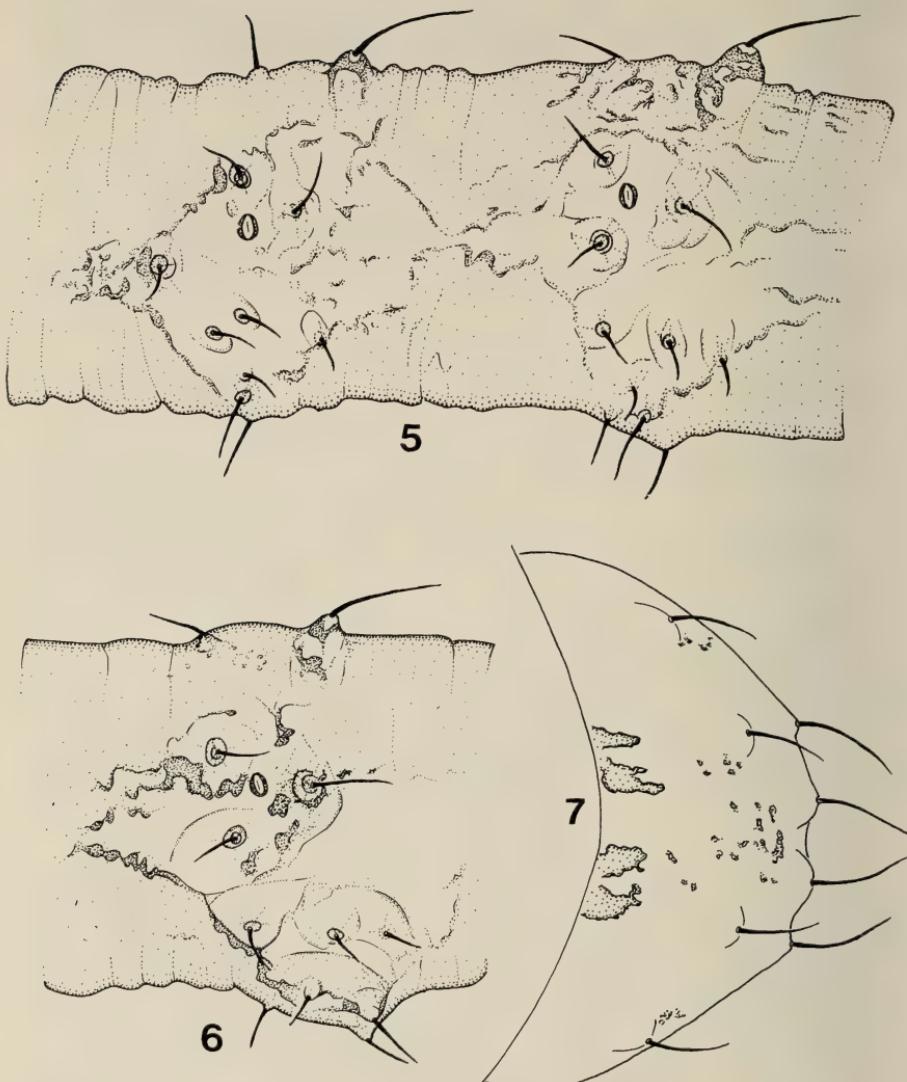
FIGS. 5–7. Larva of *H. dissociaria*. **5,** lateral view of abdominal segments 1–2, 30×; **6,** lateral view of abdominal segment 3, 30×; **7,** anal plate, 60×.

smallest (Fig. 8); antennal base with emargination between ocelli 4 and 5 (Fig. 8); mandibles with four large and five small teeth (Fig. 12); more apical mandibular seta twice length of other (Fig. 12); labrum strongly bilobed (Fig. 10); epipharynx with outer pair of heli slightly larger than inner pair, middle pair much smaller (Fig. 10); postmentum with pair of very long setae (often asymmetrical) (Fig. 11); hypopharynx heavily sclerotized; spinneret tube-shaped, slightly tapering apically (Fig. 11); labial palps long and narrow, almost length of spinneret (Fig. 11); posterior side of each maxilla with four prominent setae, most apical one smallest (Fig. 11); terminal lobe of maxilla with three setae and two papillae, most distad of each largest (Fig. 1).
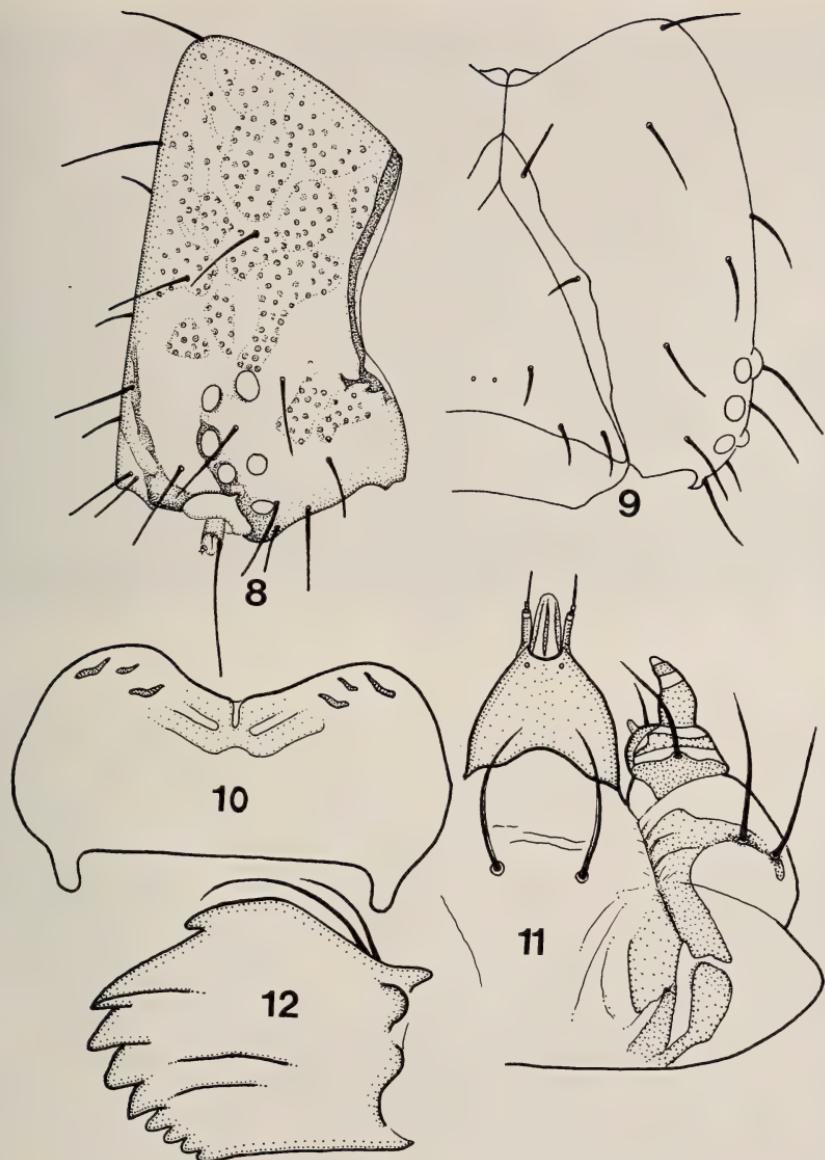
FIGS. 8–12.   Larva of *H. dissociaria*. **8,** lateral view of head, 40×; **9,** frontal view of head, 40×; **10,** epipharynx, heli and labral shape, 60×; **11,** ventral view of mentum, hypopharynx, labial palpi, spinneret and maxilla, 60×; **12,** inner view of right mandible, 60×.

Body. Length, 51 mm; width, 4.8 mm; pattern and coloration complex, individually variable (Fig. 13); integument finely granular, several grains equaling width of one seta; setae light brown, most arising from prominent chalazae: D2, L1 and SV1 largest on anterior abdominal segments (Figs. 5–6). **Dorsal view:** thorax variably patterned
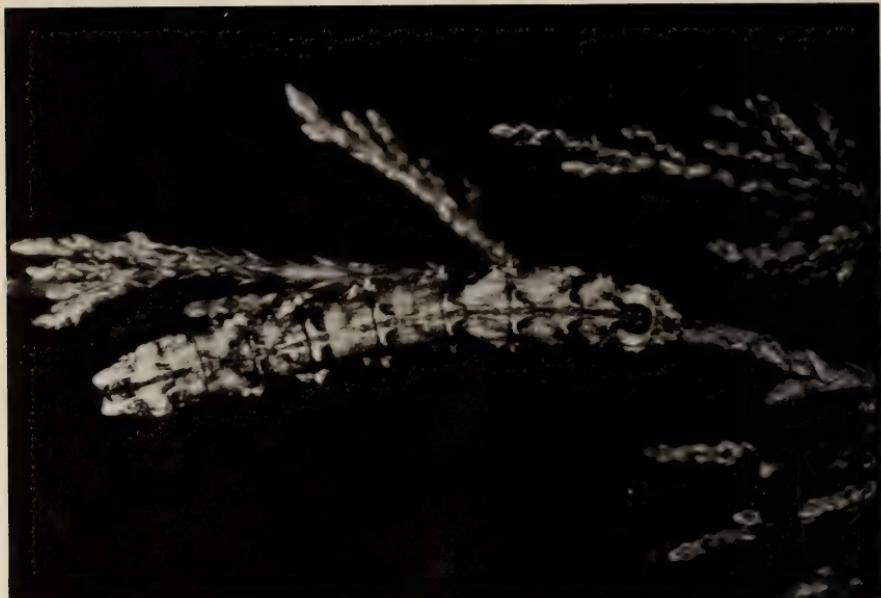
Figs. 13, 14. Larva of *H. dissociaria*. **13,** dorsal view of mature larva, Walnut Canyon, Ariz., 1.5×; **14,** adult male, Walnut Canyon, Ariz., 3.5×.

with different shades of gray and cream, with strong mesial sculpturing, particularly on prothorax; metathorax with reddish brown and gray replacing cream. Abdomen variably patterned with different shades of gray, cream and reddish brown, the cream most obvious between D2 setae, red most obvious on segments A1, A3 and A4 (strongest); pattern with diffuse, gray mid-dorsal stripe variably forking anteriorly and posteriorly on each segment, anterior fork usually stronger; forks usually meeting intersegmentally to form variable, diamond-shaped configurations of light color; horseshoe-shaped black mark on A8 with open end anteriorly directed; largest D2 tubercle on A2. **Lateral view:** thoracic coloring like that of dorsum; strong black subspiracular stripe across pro- and mesothorax (Fig. 3), basically gray below stripe and cream above; metathorax with cream centrally and suffused red and gray dorsally and ventrally. Abdomen colored similarly with red most obvious on A1, A3 and A4 (strongest); variably oblique gray and black lines or patches (exocuticular sclerotin), cream on centrally located patches between gray most obvious on A1, A2, A3 and A6, least on A4, prolegs cream colored laterally; largest L1 and SV1 chalazae on A3; peritreme black, spiracular valve pink; hypoproct longer than paraprocts. **Ventral view:** thorax variably patterned with different shades of gray and cream; leg bases increasing in size by twice that of preceding segment; thoracic leg claw dark brown, pointed, with pad in hook (Fig. 2). Abdomen with intrasegmental diamond-shaped patches outlined by gray but filled principally with red and gray in varying amounts; crochets in completely formed biordinal mesoseries, 41–45 in number on ventral proleg.

Chaetotaxy. Head: P1 and P2 rising with apical extension of each side of head (Figs. 8–9). **Abdomen:** extra SV seta on A1–6 (Figs. 4–6), migrating posteriorly on A1–3 (Figs. 5–6); SV3 seta usually bisetose or rarely trisetose on A6 (Fig. 4); remaining SV setae on A6 numbering from 9–11 (Fig. 4), in most geometrids these number 4–5; L1 seta nearly twice length of other L setae on A1–5 (Figs. 5–6); D2 seta about twice length of D1 on A1–6 (Figs. 5–6); anal plate with D2 and L1 setae slightly larger than D1 and SD1 setae (Fig. 7).

DISCUSSION AND NOTES

The mature larva is unusual in having the extra SV seta on A1–6. Designating the affinity of the extra seta to the SV setal group appears most accurate, since it migrates closer to the SV3 seta on each progressive segment and is apparently the extra seta contributing to the bisetose condition of SV3 on the ventral proleg (an L group seta would not be found here). Examination of four available *Nacophora* species, *belua* (Rindge), *cristifera* (Hulst), *mexicanaria* (Grote) and *quernaria* (J. E. Smith), revealed that the chaetotaxy of these larvae is almost identical to *H. dissociaria*. Numerous studies have been made on *N. quernaria* with no mention of the extra seta. However, McGuffin (1967) did note the extra seta (referred to as the LX seta) in *N. kirkwoodi* (Rindge). He also stated that this extra seta is not present in the first instar larva. *Nacophora* larvae are most readily separated from *Holochroa* by the presence of body papillae and microspurs, ventral branching filaments on A6–9 and larger chalazae.

McGuffin (pers. corr.) describes the chaetotaxy of *Gabriola* as being similar to that of *Nacophora*. Examination of mature larvae of *Ceratonyx arizonensis* (Capps) and *C. permagnaria* (Grossbeck) showed no extra seta. Larval specimens are not available for the other genera.

Field notes taken by Dr. R. W. Poole, Systematic Entomology Lab-

oratory, USDA, describe the egg of *H. dissociaria* as being rounded at its base and flattened on top with a smooth texture and metallic tan coloring. Eclosion occurs after 9–15 days. The first instar larva is black and white banded, with a brown head and a slightly flattened body. The larva has four instars and feeds for about one month.

ACKNOWLEDGMENTS

LITERATURE CITED

FERGUSON, D. C. 1982. [Geometridae], *in* Hodges, R. W. et al., Checklist of the Lepidoptera of America North of Mexico. E. W. Classey Limited and the Wedge Entomological Research Foundation.
MCGUFFIN, W. C. 1967. Immature stages of some Lepidoptera of Durango, Mexico. Can. Ent., 99: 1215–1229.
RINDGE, F. H. 1961. A revision of the Nacophorini (Lepidoptera, Geometridae). Bull. Amer. Mus. Nat. Hist., 123(2): 87–154.
——— 1971. A revision of the Nacophorini from cool and cold temperate southern South America. Bull. Amer. Mus. Nat. Hist., 145(4): 303–392.
——— 1974. A revision of the moth genus *Gabriola* (Lepidoptera, Geometridae). Amer. Mus. Novit., no. 2550, 24 pp.

TWO NEW SUBSPECIES OF THE *PAPILIO INDRA* COMPLEX FROM CALIFORNIA (PAPILIONIDAE)

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ABSTRACT. Two new subspecies of *Papilio indra* Reakirt are described from California. *P. i. phyllisae* is a large, widebanded subspecies from the southern Sierra Nevada, and is most closely related to *P. i. indra* populations of the central and northern Sierra Nevada; the foodplant is *Tauschia parishii*. *P. i. panamintensis*, a subspecies of the Death Valley region, has its closest affinity to *P. i. martini* of the Providence Mountains, California, and to unnamed *P. indra* segregates in southern Nevada; its foodplant is *Lomatium parryi*.

Within the state of California, geographically isolated populations of *Papilio indra* Reakirt have evolved into a number of distinctive subspecies. Over the past seventeen years, the author has sampled a large number of these populations, and an overall pattern of subspeciation has been delineated. Two distinctive segregates, one occurring in the southern Sierra Nevada and the other in the mountains of the Death Valley region, were found to be unassignable to any of the named subspecies of *P. indra* and are described below.

Papilio indra phyllisae, new subspecies

(Figs. 3–4)

Description. Male. Head, thorax as in typical *P. indra*. Abdomen black with a broad yellow lateral band. Forewing length, 35–47 mm. Tail length, 3–6 mm. Primaries, dorsal surface. Wing more elongated than typical *indra*; ground color jet black; submarginal spots pale yellow, and larger and more rounded than typical *indra*; post-median row of arrowhead-shaped markings pale yellow, and wider than typical *indra*, often twice as wide; pale yellow bars at distal end of discal cell similar in size and shape to typical *indra*. Secondaries, dorsal surface: Wing more elongated than in typical *indra*; ground color jet black; submarginal spots pale yellow, and more prominent than in typical *indra*; post-median band pale yellow, and wider than typical *indra*, often twice as wide; pattern of blue scaling and anal eyespot similar to typical *indra*. Primaries and secondaries, ventral surface: Similar to dorsal surface, except that light markings are cream and slightly larger. **Female.** Head, thorax, abdomen, wing shape, and color pattern as in male. Forewing length, 41–48 mm. Tail length, 3–7 mm.

Types. Holotype male: Butterbread Peak and ridge running to the southwest, 4900–5900′, Kern Co., California, S. 30 & S. 31, T. 29 S., R. 36 E.; ovum collected 16 May 1978 and reared to adult; adult emerged 23 March 1979. **Allotype female:** Locality data same as for holotype; larva collected 29 June 1974 and reared to adult; adult emerged 27 May 1975. **Paratypes:** 16 ♂♂, 14 ♀♀, same locality as holotype, collected as ova and larvae on 29 June 1974, 18 May 1976, 12 May 1977, 16 May 1978, and 7 May 1980, and reared to adults; adult emergence dates May 1975 to June 1980. 8 ♂♂, summit of Butterbread Peak, 5900′, Kern Co., California, 19 May 1973; 2 ♂♂, same locality, 18 May 1976. All specimens collected by J. F. Emmel.

Deposition of type material. The holotype, allotype, and 30 paratypes will be deposited in the collection of the Natural History Museum of Los Angeles Co., Los

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Angeles, California. One pair of paratypes will be deposited in each of the following collections: California Academy of Sciences, San Francisco; San Diego Natural History Museum, San Diego, California; Allyn Museum of Entomology, Sarasota, Florida; U.S. National Museum, Washington, D.C.; American Museum of Natural History, New York.

Type locality. Butterbread Peak is also spelled Butterbredt Peak on some maps. The peak is part of the extreme southern end of the Sierra Nevada, and is located about 22 airline miles northeast of the town of Tehachapi. The vegetation on the slopes of the peak consists largely of sparse Joshua Tree (*Yucca brevifolia* Engelm. in Wats.) and Juniper (*Juniperus californica* Carr.) Woodland with *Eriogonum fasciculatum* Benth., *Atriplex canescens* (Pursh) Nutt., and *Tauschia parishii* (C. & R.) Macbr.

Additional specimens examined. (All CALIFORNIA) KERN CO.: 1 ♂, Piute Peak summit, 3 July 1972; 4 ♂♂, Piute Mountain summit, 8–9 June 1974; both records leg. Jim Brock (Brock collection). TULARE CO.: 2 ♀♀, Xyz Creek, 6200′, 19–26 June 1951, leg. Chris Henne & Charles Ingham (Los Angeles County Museum). INYO CO.: ova on *Tauschia parishii*, Carroll Creek, 5800′, 16 June 1976, leg. James Haney (Haney collection); 2 ♂♂, Cottonwood Creek, 5300′, 28 May 1970, leg. Charles Hogue (L. A. Co. Museum).

Etymology. I take great pleasure in naming this subspecies after my wife, Phyllis P. Emmel, who has provided abundant support and encouragement for my studies of the *P. indra* complex.

Geographic Range, Phenology, and Life History Notes

This distinctive subspecies is found from the Piute Mountains and extreme southern Sierra Nevada of Kern Co. north to the upper Kern River drainage of Tulare Co. and along the east slope of the Sierra Nevada in Inyo Co. as far north as Whitney Portal. Emergence of adults begins in late April or early May and continues through early June. A small second brood emerges in July in most years. The apparent sole foodplant of *P. i. phyllisae* is *Tauschia parishii,* a large apiaceous species found in the California mountains from the southern Sierra Nevada to San Diego Co. The fifth-instar larvae of *phyllisae* are bright pink with black transverse bands and transverse rows of orange dots. The color pattern of the fourth-instar larvae in particular is distinctive from all other *P. indra* subspecies. The early stages will be described in detail in a separate paper.

Remarks

P. i. phyllisae superficially resembles *P. i. nevadensis* Emmel & Emmel (1971), which is also a large, somewhat broad-banded subspecies. Detailed studies of *nevadensis* and other southern Great Basin *P. indra* populations (J. F. Emmel & Bruce Griffin, unpublished data) indicate that *nevadensis* is most closely related to an unnamed set of *indra* populations in southern Nevada. Larvae and adults of these *indra* from central and southern Nevada show a closer affinity to *P. i. minori* Cross, *P. i. kaibabensis* Bauer, and *P. i. martini* Emmel & Emmel (Emmel & Emmel, 1964, 1967, & 1968) than to nominate *P. indra. P. i. phyllisae,* in contrast, is most closely related to *P. i. indra* of the central and northern Sierra Nevada. This assessment is

FIGS. 1–6. Adults of *P. indra*; left half of each figure shows dorsal surface, right half shows ventral surface. **1–2**, *P. i. indra*, male (**1**), female (**2**); COLORADO: Boulder Co.; Lefthand Canyon, ex ova from female taken 10 June 1972 by Don Eff. **3–4**, *P. i. phyllisae*, new subspecies, holotype male (**3**) and allotype female (**4**). **5–6**, *P. i. panamintensis*, new subspecies, holotype male (**5**) and allotype female (**6**).

based on the similarity of the immature stages of the two subspecies and on the existence of occasional *phyllisae-indra* intermediates in *P. i. indra* populations just north of the range of typical *phyllisae*. It is of interest to note that the range of *phyllisae* correlates well with the known range of *Tauschia parishii* in the southern Sierra Nevada, while typical *indra* is confined to the known range of its host, *Pteryxia terebinthina* (Hook.) Coult. & Rose, in the central and northern Sierra Nevada; the ranges of the two foodplants do not overlap (Munz, 1963).

Papilio indra panamintensis, new subspecies

(Figs. 5–6)

Description. Male. Head, thorax as in *P. i. indra.* Abdomen black, with a virtual absence of yellow scaling in most specimens; when yellow scaling is present, it occurs as a small patch laterally on the eighth abdominal segment. Forewing length, 37–41 mm. Tail length, 3–5 mm. Primaries, dorsal surface: Wing more elongated than typical *indra*; ground color jet black; submarginal spots pale yellow, more prominent than in typical *indra*, and tending to retain their crescent shape; post-median row of pale yellow markings slightly wider than in typical *indra*, and tending to be round or oval rather than arrowhead-shaped; medial apices of post-median spots sprinkled with black scales; distal end of discal cell totally lacking the pale yellow bars which are present in typical *indra*. Secondaries, dorsal surface: Wing more elongated than in typical *indra*; ground color jet black; pale yellow submarginal spots similar to or less prominent than in typical *indra*; pale yellow post-median band of same width as typical *indra* in two cells nearest costal margin, but posteriorly this band rapidly becomes obsolescent or absent; pattern of blue scaling and anal eyespot similar to typical *indra*, but blue scales reduced in number. Primaries and secondaries, ventral surface: Similar to dorsal surface, although light markings are cream and somewhat more extensive. **Female.** Head, thorax, abdomen, wing shape, and color pattern as in male. Forewing length, 42–50 mm. Tail length, 4–7 mm.

Types. Holotype male: Thorndike Campground, Wildrose Canyon, 7400′, Panamint Range, Inyo Co., California, S. 35, T. 19 S., R. 45 E.; larva collected 16 June 1974 and reared to adult; adult emerged 24 May 1975. **Allotype female:** Locality data same as for holotype; larva collected 20 June 1976 and reared to adult; adult emerged 5 June 1977. **Paratypes:** (All Inyo Co., California) 1 ♂, 4 ♀ ♀, same locality as holotype, larvae collected 16 June 1974 and 20 June 1976 and reared to adults; adult emergence dates June 1975 to May 1977. 2 ♂♂, 1 ♀, Water Canyon, 7200′, above Surprise Canyon, Panamint Range, S. 2, T. 21 S., R. 45 E.; ova and larvae collected 15 June 1974 and reared to adults; adult emergence dates June 1975. 1 ♂, Rogers Peak summit, 9994′, Panamint Range, S. 3, T. 20 S., R. 45 E., 10 July 1978. All of the above leg. J. F. Emmel. 1 ♂, summit of Telescope Peak, 11,049′, Panamint Range, 25 May 1974, leg. Steve Bellinger. 1 ♂, Mahogany Flat, 8143′, Panamint Range, 25 May 1974, leg. James Wells. 1 ♂, Mahogany Flat, 8300′, 11 August 1974, leg. James Wells.

Deposition of type material. The holotype, allotype, and 9 paratypes will be deposited in the Natural History Museum of Los Angeles Co., Los Angeles, California. Three paratypes (the last three listed under Types) are in the National Park Service collection at Park Headquarters, Death Valley National Monument, Death Valley, California.

Type locality. Wildrose Canyon is a large canyon on the west slope of the Panamint Range in the Death Valley region of Inyo Co. Thorndike Campground is located in the upper part of this canyon at the 7400-foot contour. The vegetation in the type locality is Pinyon-Juniper Woodland with *Artemisia tridentata* Nutt., *Cercocarpus ledifolius* Nutt., *Cowania mexicana* D. Don var. *stansburiana* (Torr.) Jeps., *Eriogonum umbellatum* Torr. var. *subaridum* Munz, and *Lomatium parryi* (Wats.) Macbr.

Additional specimens examined. (All Inyo Co., California) 1 ♂, Tin Mountain summit, 8953′, Cottonwood Mountains, 2 July 1979, leg. J. F. Emmel & O. Shields (Emmel collection). 1 ♂, Last Chance Spring, Last Chance Range, 5600′, S. 2, T. 8 S., R. 39 E.; larva collected 27 May 1974 and reared to adult; adult emerged 2 June 1975; leg. J. F. Emmel (Emmel collection). 1 ♂, ridge above Last Chance Spring, 7000′, Last Chance Range, 21 June 1977, leg. Derham Giuliani (Emmel collection).

Etymology. The subspecies is named after the greater Panamint Range which forms the entire western side of Death Valley. This range includes, besides the Panamint Range proper, the Cottonwood Mountains and the Last Chance Range to the north.

Geographic Range, Phenology, and Life History Notes

Populations of *P. i. panamintensis* are known from the Panamint Range, Cottonwood Mountains, and Last Chance Range in Inyo Co., California. *P. indra* larvae recently collected by the author in the Grapevine Mountains and Nopah Range, Inyo Co., also probably represent this subspecies. Emergence of adults takes place in May and early June, with a peak flight in late May. A small second brood flies in late July and early August in years of above-average winter rainfall. The sole foodplant is *Lomatium parryi* (Apiaceae), which ranges from eastern California to Nevada, Utah, and extreme northern Arizona. The early stages of *panamintensis*, to be described in detail in a separate paper, closely resemble those of *P. i. martini* and the unnamed southern Nevada *P. indra* segregates.

Remarks

This subspecies appears to be most closely related to *P. i. martini* of the Providence Mountains, San Bernardino Co., California. Important points of distinction are as follows: The wings in *panamintensis* have a deep, jet black ground color, whereas in *martini* the ground color is dull black; the light markings on the wings are pale yellow in *panamintensis* and cream in *martini*; the forewing post-median row of markings is much narrower in *martini,* often obsolescent; whereas, it is well-developed in *panamintensis*; the submarginal spots on both wings are reduced in *martini* and usually enlarged in *panamintensis*; the blue scaling on the hindwing is more prominent in *martini* than in *panamintensis*.

P. i. panamintensis was first taken by Stan Dvorak, who collected a male specimen on Telescope Peak in the Panamint Range on 9 May 1970. Subsequently, specimens were collected in May 1974 by James Wells and Steve Bellinger in the Panamint Range, and by the author in the Last Chance Range. It is remarkable that no earlier specimens are known, in view of the fact that the Panamints have been fairly frequently collected by California lepidopterists since the mid-1930's.

LITERATURE CITED

EMMEL, J. F. & T. C. EMMEL. 1964. The life history of *Papilio indra minori.* J. Lepid. Soc., 18:65–73.
—— 1966. A new *Papilio* from the Mojave Desert of California (Lepidoptera: Papilionidae). Entomol. News, 77:57–63.
—— 1968. The population biology and life history of *Papilio indra martini.* J. Lepid. Soc., 22:46–52.
EMMEL, T. C. & J. F. EMMEL. 1967. The biology of *Papilio indra kaibabensis* in the Grand Canyon. J. Lepid. Soc., 21:41–48.
—— 1971. A new subspecies of *Papilio indra* from central Nevada (Lepidoptera: Papilionidae). Pan-Pacific Entomol., 47:220–223.
—— 1974. The biology of *Papilio indra nevadensis* (Papilionidae) in Nevada. J. Lepid. Soc., 28:107–114.
MUNZ, PHILIP A. 1963. A Flora of California. University of California Press, Los Angeles. 1681 pp.

BOOK REVIEW

THIS IS HONG KONG: BUTTERFLIES, by Gweneth and Bernard Johnston. 1980. E. W. Classey Ltd., Faringdon, Oxon, England. 224 pp., 28 color plates. Price: $28.80 postpaid.

This book is largely a pictorial treatise on butterflies, but a very good one for its genre, and one that I thoroughly enjoyed reading. It is divided into major sections dealing with such topics as the place of butterflies in the animal kingdom, the problems and strategies for survival of the various life stages, the major families of Hong Kong butterflies, rearing, and the past collecting history of the island. Sections dealing with the life stages and survival strategies are then sub-divided to treat each life stage (from egg through imago) separately. The text describing the butterfly families gives the reader a general survey of the habits and preferred habitats for the members of each family, and only mentions specific butterflies where they are especially common or outstanding in their appearence.

My only real criticism of the book is that it is too general in nature to be considered a comprehensive field guide to the island's fauna. However, the authors make a point of disclaiming the book as a great scientific work. Still, the book is of some scientific value for it deals with a geographical area that is, to the best of my knowledge, poorly addressed in previous scientific literature. There is a checklist in the appendices listing all 192 recorded Hong Kong species of butterflies accompanied by their English common names, their Chinese common names in native characters, and their larval food-plants (where known). It is no great surprise that the fauna of Hong Kong shows affinities to those of Japan and Formosa, both of which have been well-documented and well-studied. So, armed with the Johnston's checklist, the life history data on the various species from these other Asian regions, one could conceivably utilize this work as a field guide of sorts.

The prose style of the text has a decidedly British flavor, but is generally easy to read and thoroughly enjoyable. A minor criticism: the text is sprinkled with the usual anthropomorphisms so commonly resorted to by writers when dealing with such wondrous creatures as butterflies. Their references to nymphalids "in ecstacy at the taste" of flower nectar in the chapter dealing with that family should adequately illustrate my point. However, when one considers the splendor and unique habits of the authors' subject matter, it is easy to see how one is tempted to resort to such non-scientific descriptions. I must confess that I have used some of the very same descriptions myself, and, while they do not necessarily reflect scientific truth, they certainly lend impact to the text for the average reader. Along these same lines, the book's tenth chapter deals with butterflies as depicted in Chinese culture, customs, and legends. In this chapter, the authors relate several Chinese proverbs which demonstrate the reverence that ancient philosophers had for butterflies. These philosophers were as given to ascribing humanlike attributes to these beautiful creatures in their day as we continue to be in ours.

The greatest strength of this book lies in the excellent quality of its color photographs. All of the chapters are profusely illustrated in color, showing butterflies in their natural state. The selections chosen by the authors depict both the main features and the incredible diversity within each family. Many of the larvae and pupae of the island's butterflies also are figured, some for the first time in any popular work. Additionally, there are 28 color plates illustrating set specimens of 150 of the island's 192 species. The quality of these plates is also extremely good.

Overall, this book is well worth its high cost, even if only for the beautiful color photography. It will certainly occupy a prominent place in my library, as it will, I am sure, in the libraries of others who decide to purchase it. It is available through E. W. Classey's U.S. representative at P.O. Box 1062, San Marcos, California 92069.

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DISTRIBUTION OF CECROPIA MOTH (SATURNIIDAE) IN CENTRAL ILLINOIS: A STUDY IN URBAN ECOLOGY

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ABSTRACT. Searches for cocoons and trapping adult males with virgin females showed that, in central Illinois, *Hyalophora cecropia* is rare in forests and old urban residential areas, uncommon in willows and other trackside and roadside vegetation, but abundant in new urban residential areas. The new residential areas built on crop fields, and the tracksides and roadsides have small trees and shrubs and resemble an early stage in succession. The forests and old residential areas have large trees and shrubs, and resemble a late stage in succession. We suggest that the cecropia moth is a fugitive species that "flees" to early stages in the succession. The availability of food plants cannot be the cause since acceptable hosts occur in all of the areas. The difference in the population size between rural and urban areas is at least partly explained by a difference in small mammal populations. *Mus musculus*, the most commonly trapped small mammal in residential areas, will eat naked cecropia pupae in the laboratory, but will not open cocoons to obtain the pupae. *Peromyscus leucopus* and *P. maniculatus*, the most commonly trapped small mammals in rural areas, readily open cecropia cocoons in the laboratory. Low-spun cocoons with injury typical of *Peromyscus* are frequent in tracksides and roadsides, but are almost never found in town. Woodpeckers prey heavily on both urban and rural high-spun cocoons. The small cecropia population in old residential areas and woodlands may be explained by the presence of caterpillar-feeding birds that are absent or scarce in the other areas. Cocoons were placed for the winter in woodlands to determine if mice or woodpeckers would attack them despite the absence of a natural cocoon population. Almost none of the cocoons taped near ground level were attacked by mice or other predators. Cocoons taped high in saplings were seldom attacked by woodpeckers, but were heavily attacked by an unidentified predator, probably the fox squirrel, *Sciurus niger*.

In 1965 we began long term studies of the cecropia moth, *Hyalophora cecropia* (L.) (Saturniidae). Intensive searching for cocoons in Champaign Co., Illinois, showed them to be rare in rural areas, almost absent in woodlands, and scarce in roadside and trackside woody vegetation. They were abundant in new urban residential areas but scarce in old urban residential areas. We report the results of systematic searching for cecropia cocoons in the winter and of trapping adult males in the summer, and discuss the distribution of this species in relation to land use, vegetative cover, and predation pressure.

Champaign Co., in east central Illinois, is highly agricultural. Over 90% of its land is in field crops; the original prairie and forests have almost disappeared. The towns and cities, planted with ornamental trees and bushes, are thus islands of urban forest in a sea of cropland. Natural forests are limited to a few small upland tracts and narrow

strips along the larger rivers. A few small woody plants grow on railroad and highway rights-of-way and in fence rows.

Several reports indicate that cecropia is generally uncommon in rural and wild areas, but that it may have unusually high populations in some urban areas. Smith (1899 and 1908) found cecropia to be particularly abundant in cities in New Jersey and on Long Island, New York. Thompson & Fiske (1909) found large numbers of cocoons only by collecting in cities in New Hampshire, Massachusetts, New York and New Jersey. Porter (1912) found many cocoons in Indianapolis, Indiana but reported only a few from rural Indiana. Cocoons were reported to be abundant in Chicago, Illinois, by Downing (1921) and Marsh (1937) and in Champaign and Urbana, Illinois, by Sternburg & Waldbauer (1969) and Waldbauer & Sternburg (1973). Few workers report cecropia to be abundant in rural or wild areas. Maughan (1906) found many cocoons in a swampy grove in Ontario. In reporting a find of 79 cocoons in a grove in rural Ohio, Miller (1927) remarked upon his delight at finding so many cocoons in a natural environment. Cecropia has also extended its range westward into the plains, coinciding with the movement of settlers (Sweadner, 1937). These observations and our own suggest that the founding of towns with shade trees and shrubs provided habitats that can support much larger cecropia populations than are usually found in wild or rural habitats.

Cecropia is univoltine, overwintering as a diapausing pupa in a tough cocoon firmly attached to the food plant or to a nearby shrub. The emergence curve of the adults is bimodal, with one group emerging in late May and another in late June (Sternburg & Waldbauer, 1969; Waldbauer & Sternburg, 1973; Waldbauer, 1978). The adults do not feed and have an average life span of only about ten days (Rau & Rau, 1914). The larvae feed on a wide variety of woody plants, and spin and pupate in late summer or early fall (Waldbauer & Sternburg, 1967b; Ferguson, 1972; Scarbrough et al., 1974). Cecropia occurs in most of the eastern United States, from southern Canada to the Gulf States and from the east coast to the Rockies (Ferguson, 1972).

STUDY AREAS AND METHODS

During the winters of 1965–66, 1967–68 and 1968–69 we collected cocoons extensively in Champaign Co. Collections were made throughout the contiguous cities of Urbana and Champaign, records being kept by street address so that we could plot distributions. We also collected from the woody plants along 93 km of railroad tracks north and east of Urbana and Champaign, including about 45 linear km of stands of *Salix interior* Rowlee (sandbar willow). Two natural forests, Hart and Trelease Woods, were also searched for cocoons.

The distribution of adult cecropia was surveyed in 1968 and 1969 (Sternburg & Waldbauer, 1969; Scarbrough, 1970) by luring wild males to traps baited with virgin females. Locations of our five traps were: two, 6.8 km apart, in urban residential areas near opposite edges of the Champaign-Urbana metropolitan area, one of them 1.6 km west of the east edge of Urbana in an area of intermediate age and the other 1.6 km east of the west edge of Champaign in a recently built area; three in nearby rural areas, one at the south edge of Trelease Woods, another 45 m into the east edge of Hart Woods, and the last near a stand of sandbar willow on the railroad right-of-way near Mayview (see below for locations). The traps ran continuously from 13 May to 20 July each year, i.e., until about 12 days after the last moth was caught. However, no traps were at Mayview or Hart Woods in 1968. Each trap was constantly baited with two or three newly emerged females that were replaced every third day and kept in cages in the traps, thus preventing mating and assuring continued pheromone release. Traps were checked daily. Males captured for the first time were marked with an identifying number and released in the morning at the trap site where they had been caught (Sternburg & Waldbauer, 1969; Scarbrough, 1970).

Areas Searched

Trelease Woods, 5 km northeast of Urbana and surrounded by crop-fields at the time of the study is a 12 hectare remnant of a prairie grove. It is a mixed mesophytic stand with an abundance of sugar maple (*Acer saccharum* Marshall) and hackberry (*Celtis occidentalis* L.), and with an understory dominated by pawpaw (*Asimina triloba* (L.) Dunal) and thornapple (*Crataegus* sp.). Food plants of cecropia commonly found include: wild black cherry (*Prunus serotina* Ehrh.), wild plum (*P. americana* Marsh), smooth sumac (*Rhus glabra* L.), basswood (*Tilia americana* L.), elderberry (*Sambucus canadensis* L.), sandbar willow (*Salix interior* Rowlee), silver maple (*Acer saccharinum* L.) and *Crataegus* sp.

Hart Woods, 6.5 hectares and on the Sangamon River near Mahomet, is well drained, somewhat xeric, and contiguous with a much larger area of bottomland forest. White and black oaks (*Quercus alba* L. and *Q. velutina* Lam.) dominate the upland; red oak (*Q. rubra* L.) occurs on the slopes, and silver maple, one of cecropia's favorite food plants, is abundant on the adjacent bottomland. Wild black cherry and elderberry, both food plants for cecropia, are common in most of the understory.

Railroad rights-of-way, about 4.5 m wide on each side of the tracks, have mostly herbaceous plants, but there are also scattered cecropia food plants, wild black cherries, box-elder maples (*Acer negundo* L.),

red osier dogwoods (*Cornus stolonifera* Michx.) and elderberries. Sandbar willow abounds in low areas, especially near Mayview, a cluster of about a dozen houses nearly 5 km east of Urbana. The tracksides are bordered by field crops or, in a few places, by osage oranges [*Toxylon pomiferum* (Raf.)] hedgerows.

The older sections of Champaign and Urbana, business districts and the adjacent residential areas, were settled in the late 1800's and early 1900's (Smith, 1957). Trees and shrubs in these areas are mostly old and large, except for trees planted after 1953 to replace elms (*Ulmus americana* L.) lost to disease. In aerial photographs of these old areas, the crowns of trees are seen to overlap and largely obscure the roofs of buildings. Both cities have grown constantly since the late 1940's, and residential areas, recently built on treeless farmland, are located at their peripheries. Trees here are often widely spaced and usually small; in aerial photographs the crowns of trees do not overlap the roofs of buildings. Areas of intermediate age with trees and shrubs of moderate size occur between the old and new areas. In aerial photographs most buildings in these areas are but partially obscured by trees.

In addition to a widespread search for cocoons throughout Urbana and Champaign, the six plots (described below) in old and new residential areas were exhaustively searched to obtain the most quantitative measure possible of relative abundance (Scarbrough, 1970).

Comparison of the Woody Plants of Old and New Residential Areas

The food plants available to cecropia in old and new urban residential areas were compared by censusing all woody plants in three sample plots in each of the two types of areas (Scarbrough, 1970). Intermediate areas were not examined. Preliminary observations showed no differences in the trees and shrubs in back and in front of houses. Therefore, each plot consisted of 300 contiguous front yards and the adjacent street-side plantings. Their areas were 22, 15, and 15 hectares, respectively, for plots A, B and C in new neighborhoods; and 13, 14, and 17 hectares, respectively, for plots D, E and F in old neighborhoods. The relative density of each species of woody plant was calculated as:

$$\text{Relative density} = \frac{\text{total number of individuals of one species}}{\text{total number of individuals of all species}} \times 100$$

Predation Studies

Waldbauer & Sternburg (1967a) found that most of the cecropia pupae in cocoons on trees and on the upper branches of shrubs in

Champaign and Urbana had been killed by downy woodpeckers, *Dryobates pubescens* (L.), and hairy woodpeckers, *D. villosus* (L.), during winter. The seasonal progression of predation and whether or not a comparably high level of predation would occur again were determined by observing 250 naturally occurring cocoons in the six plots. These cocoons, left *in situ*, were checked for the easily identified woodpecker damage every two weeks from 12 October to 13 May, when new leaves appeared on the trees (Scarbrough, 1970).

We also attempted to measure the potential extent of woodpecker predation on pupae in woodlands where cecropia cocoons rarely occur. Cocoons with living pupae and still attached to twigs were taped (General Electric plastic electrical tape) to thin pawpaw or wild black cherry saplings 3 to 6 m tall in Trelease and Hart Woods. The saplings were bent down and a cocoon was taped snugly to the trunk or a main branch. When the saplings were relased the cocoons were at heights comparable to those of cocoons in urban areas. To control for the effects of taping, cocoons were similarly placed in an old residential area in Champaign where woodpecker predation was known to occur. They were taped to saplings when possible, but most had to be taped to low branches of large trees. Fifty cocoons were placed one to a tree and not less than 45 m apart in each of the three areas. They were checked for damage every two weeks, beginning on the first of November, until the last cocoon had been attacked (Scarbrough, 1970).

The mice *Peromyscus leucopus* (Rafinesque) and *P. maniculatus* (Wagner) prey extensively on cecropia pupae in trackside and roadside areas, leaving an easily recognized injury (Scarbrough et al., 1972). An experiment similar to the one described above determined the potential predation by these mice on cecropia cocoons in Trelease and Hart Woods. Cocoons still attached to twigs were taped to shrubs or tree sprouts as near the ground as possible, the usual position of wild cocoons attacked by mice. Cocoons to control for the effect of taping were similarly placed in two areas where predation by mice was known to occur, the trackside vegetation near Mayview and a row of *Cornus stolonifera* along Interstate 74 near Champaign. Twenty were placed in each location, one to a bush or tree, about 9 m apart. The cocoons were checked monthly from 15 November to 15 May.

RESULTS

Distribution of Cecropia: Rural vs. Urban Areas

Cocoons were scarce in rural areas (Table 1). None were found in Hart Woods, and only one in Trelease Woods. Ninety-three linear km of trackside vegetation examined in 1968–69 yielded 196 cocoons,

TABLE 1. Numbers of the current year's cocoons of *Hyalophora cecropia* (L.) found in urban and rural areas of Champaign Co., Illinois, and the numbers of *H. cecropia* males caught for the first time in the same areas in traps baited with virgin female *H. cecropia*.

	Rural areas			Urban areas
	Mayview trackside	Hart Woods	Trelease Woods	Champaign and Urbana
Cocoons found				
1967–1968	—	0	0	721
1968–1969	92	0	1	980
Males captured				
1968	—	—	32	1033*
1969	139	14	41	1749

* Data from Sternburg & Waldbauer (1969).

47% (92) from the 6.4 km strip of sandbar willow near Mayview, 39% from other sandbar willow thickets, and 15% from other species of woody plants. Only twelve cocoons with pupal exuviae, and thus, at least one year old, were found at the Mayview site in 1968–69.

Cecropia was, however, abundant in urban areas. In 1967–68 we found 721 cocoons, and in 1968–69 we found 980 within the limits of Urbana and Champaign (Table 1). They were collected only from street sides and front yards. Cocoons in back yards were not disturbed; the males that eventually emerged from them were sampled by means of the traps.

The large number of males caught confirms the abundance of cecropia in this urban area (Table 1). In 1968 there were 1033 previously uncaptured males caught in two traps in the urban area, but only 32 were caught in the one trap at Trelease Woods. Similarly, in 1969 there were 1749 previously uncaptured males caught in two urban traps, but only 194 were caught in three rural traps. Cocoon collections indicated that urban cecropia outnumbered rural cecropia by 5:1; trapping indicated a ratio of 9:1. Trapping is probably the more sensitive sampling method, but it probably overestimated the rural population, because the Mayview trap was near the only known large concentration of rural cecropia cocoons. Nevertheless, the results of the two methods agree fairly closely and leave little doubt that urban cecropia greatly outnumbered rural cecropia.

The rural population may be partly maintained by moths from the urban area. About 12% of the marked males captured at Mayview had been released at Urbana and about 4% at the Champaign trap. About 44% of the marked males captured at Trelease had been released at the Urbana trap (Table 2). Thus, it appears that a significant number

TABLE 2. Sites of release and recapture of male *Hyalophora cecropia* (L.) recaptured in 1969.

Release site	Site of recapture				
	Trelease Woods	Mayview	Hart Woods	Urbana	Champaign
Trelease Woods	6	15	0	0	0
Mayview	3	51	0	1	0
Hart Woods	0	0	2	0	0
Urbana	7	9	0	336	16
Champaign	0	3	0	6	767
Total	16	78	2	343	783

of males, and possibly females, move from the urban to the rural habitat. On the other hand, only one male released at a rural trap was recaptured in the urban area.

Distribution of Cocoons within the Urban Area

The locations of the cocoons collected in all areas of Champaign and Urbana during the winters of 1965–66, 1967–68 and 1968–69 were plotted on separate city maps. Fig. 1 shows that most of the cocoons collected in 1967–68 came from new residential areas at the periphery of the cities, particularly in the southwest quadrant where the most extensive new areas occurred. The maps for 1965–66 and 1968–69 show almost identical distributions (Scarbrough, 1970). Table 3 shows the distribution by old, new and intermediate residential areas of all cocoons found from 1965 to 1969. From 66% to 80% were found in new areas, 16% to 23% in intermediate areas, but only from 4% to 10% in old areas. Furthermore, most of the cocoons from old areas were from sites adjacent to new or intermediate areas.

A more accurate estimate of this differential distribution was obtained by making an exhaustive search for cocoons in the six plots in old and new residential areas during the three winters from 1967 to

TABLE 3. Distribution in old, intermediate, and new residential neighborhoods in Champaign and Urbana of all cocoons of *H. cecropia* collected during three winters.

Neighborhoods	1965–66 Cocoons		1967–68 Cocoons		1968–69 Cocoons	
	No.	%	No.	%	No.	%
Old	47	10.5	47	5.7	42	3.9
Intermediate	103	23.1	145	17.6	172	16.2
New	296	66.3	631	76.6	844	79.8
Total	446		823		1058	

TABLE 4. The number and percentage of cocoons collected in six sample plots in old and new residential areas in Champaign and Urbana in each of three years. Percentages are based on the total number of cocoons collected each year in these plots.

Plots	1967–68 Cocoons		1968–69 Cocoons		1969–70 Cocoons	
	No.	%	No.	%	No.	%
New areas						
A	162	56.8	186	36.7	441	46.0
B	32	11.2	171	33.8	133	13.9
C	69	24.2	129	25.5	330	34.4
	263	92.2	486	96.0	904	94.3
Old areas						
D	4	1.4	4	0.8	17	1.8
E	11	3.8	15	2.9	31	3.2
F	7	2.5	1	0.2	6	0.6
	22	7.7	20	3.9	54	5.6

1970. In these plots well over 90% of the population was concentrated in the new residential areas; from 3.9% to 7.7% occurred in old areas (Table 4). These data are in close agreement with Table 3 where, excluding data from intermediate areas, about 7.1% of the cocoons came from old areas. Cocoons taken in neighboring cities of the county were also found almost exclusively in new residential areas.

Woody Plants of Old and New Residential Areas

There is little difference in the species of trees that are available to cecropia in old or new residential areas (Table 5). Many of them are preferred hosts (Waldbauer & Sternburg, 1967b, and Scarbrough et al., 1974). Although there were some variations between areas, silver maple was overall the most abundant tree. In two of the new residential plots, its relative density was over 26%, averaging 2 trees per hectare. In another new plot, its relative density was only 9%, with 0.4 trees per hectare; in this plot sugar maple was most abundant. Silver maple was also the most abundant tree in old areas, with relative densities of about 20% (2 trees per hectare) except in one plot where sugar maple was more abundant at a relative density of 25%.

The density of all trees, irrespective of species, did not vary much either. In the new areas there were 56.6, 44.4, and 45.2 trees per hectare in plots A, B and C, respectively; in the old areas there were 52.3, 37.7, and 35.2 trees per hectare in plots D, E and F, respectively. A much larger total amount of foliage was available in the old residential areas, because the trees were much larger.

There were no significant differences in the species of shrubs pres-

TABLE 5. The relative density of trees in the six sample plots in old and new neighborhoods of Champaign and Urbana, Illinois.

Tree species	New neighborhoods			Old neighborhoods		
	A	B	C	D	E	F
Acer saccharinum L.	9.0	28.2	26.0	20.2	20.2	13.1
*A. saccharum Marsh.	3.6	3.2	1.1	12.2	13.0	25.4
A. rubrum L.	8.3	8.4	2.0	1.3	3.8	7.5
*A. platanoides L.	1.8	1.4	2.8	0.9	4.8	6.7
Prunus spp.	1.8	0.4	1.2	3.6	1.0	2.5
Malus spp.	9.0	6.6	6.4	3.0	3.6	2.5
Crataegus spp.	0.7	2.2	0.0	0.4	0.0	0.0
Betula pendula Roth	4.2	1.4	2.4	1.0	1.2	0.6
B. papyrifera Marsh.	4.7	0.6	5.4	1.0	1.5	0.4
B. populifolia Marsh.	9.7	3.5	5.0	0.3	2.4	1.7
Platanus occidentalis L.	5.0	13.7	15.3	5.4	4.1	5.2
*Liquidambar styraciflua L.	4.4	3.5	3.2	0.9	0.8	1.0
*Ulmus spp.	2.2	4.5	1.5	12.1	3.2	0.8
*Celtis occidentalis L.	0.8	0.0	0.3	4.4	2.4	2.7
Quercus spp.	5.8	3.1	4.0	4.4	10.0	4.2
Fraxinus spp.	4.7	5.7	10.2	9.8	6.8	7.1
Cornus florida L.	2.4	0.8	0.9	0.2	0.4	0.8
Gleditsia triacanthos L.	7.9	2.1	4.6	1.6	3.5	4.4
*Ailanthus altissima Swin.	0.0	0.0	0.0	4.6	0.6	2.3
Others	14.0	10.4	7.9	12.5	14.0	11.0

* Species on which cecropia seldom or never occurs or on which the survival rate of first instars was found to be abnormally low (Scarbrough et al., 1974).

ent in the six plots. The most common were various species of juniper (*Juniperus* spp.), yew (*Taxus* spp.), spirea (*Spiraea* spp.), and privet (*Ligustrum vulgare* L.). Dense coniferous trees, some shrubby, included various pines (*Pinus* spp.), spruces (*Picea* spp.), and white cedar (*Thuja occidentalis* L.). Many cocoons were found on these plants each year. Previous experiments showed that these plants (except for spirea) are not capable of supporting normal growth by first or fifth-instar cecropia larvae (Scarbrough et al., 1974); thus, the larvae must have migrated to these plants from other plants just before spinning.

Other shrubs that are food plants for cecropia occurred sporadically in the sample plots, including lilac (*Syringa vulgaris* L.), cotoneaster (*Cotoneaster* spp.), tall hedge (*Rhamnus frangula* L.) and red-osier dogwood. Their densities were low, but they frequently harbored cocoons.

Although old and new residential areas did not differ much in the density or species composition of their woody vegetation, there were major differences in the age of the trees and in the proximity of shrubs to trees, the latter due to a change of fashion in landscaping. In new areas the trees were young, between 2 and 10 m tall, and often located

FIG. 1. The distribution of the cocoons of *Hyalophora cecropia* found in Champaign and Urbana in 1967–68.

near the center of a lawn within a few meters of shrubs or with shrubs at their base. The proximity of shrubs to host trees probably increases the survival of migrating larvae by providing nearby safe sites for cocoon spinning (Scarbrough et al., 1977). In old areas the trees were very large, usually at least 20 m tall, and generally located along the margins of lawns and streets. Shrubs and trees were generally farther apart than they were in new areas.

Predation Studies

The seasonal progression of woodpecker predation on 250 cocoons in urban trees is shown in Fig. 2. Predation began shortly before the leaves began to drop in the fall. The first cocoons attacked were not concealed by leaves but were exposed on the trunk or on short spurs originating from the trunk. At this early date, cocoons on twigs and branches were still hidden by leaves and apparently not visible to woodpeckers.

The rapid rise in predation rate coincided with leaf fall, which began in the last week of October. Most leaves had fallen by mid-November and the trees were almost completely bare by the beginning of December. The rate of woodpecker attacks remained fairly constant through most of the winter and declined in early spring; the attacks had stopped by 29 April. The decline was no doubt due to the in-
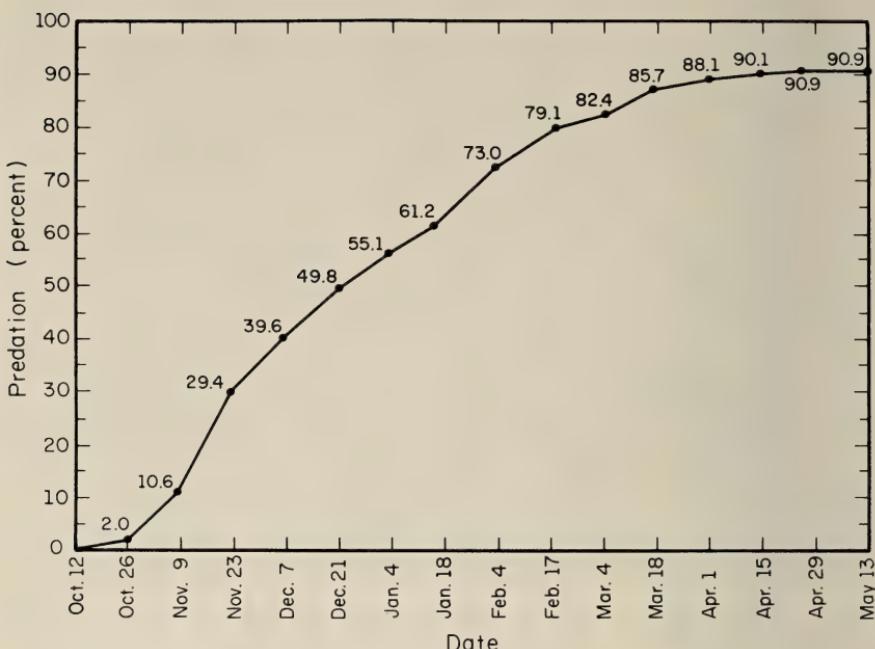
FIG. 2. The rate and seasonal progression of predation by woodpeckers on a group of 250 naturally occurring cocoons of *Hyalophora cecropia* on the branches of trees in urban residential areas of Champaign and Urbana in 1969–70.

creased difficulty the birds had in locating the few remaining unattacked cocoons. Almost 91% of the cocoons under observation were successfully attacked by woodpeckers, which agrees closely with the observation by Waldbauer & Sternburg (1967a) that 86.5% of the cocoons in trees had been attacked. Cocoons spun in evergreen shrubs or near ground level in deciduous shrubs or suckers at the bases of trees were virtually exempt from predation by woodpeckers.

Only two of the cocoons taped high in woodland trees were attacked by woodpeckers, one each at Trelease and Hart Woods. In addition, one naturally occurring cocoon attacked by a woodpecker was found at Trelease Woods. Woodpecker attacks on taped cocoons, as well as the other attacks mentioned below, occurred some time between the last week of December and 21 January. Woodpecker predation on the control cocoons taped to trees in old urban areas began much earlier and had reached 78% by 21 January. Downy and hairy woodpeckers are common in both Trelease and Hart Woods, as well as in both old and new urban areas. (Downy woodpeckers also occur in the trackside and roadside areas.) It seems likely that the forest-dwelling woodpeckers were slow to attack the taped-up cocoons, because they had

had little or no previous experience with cecropia cocoons. Whether or not the woodland woodpeckers would eventually have attacked more cocoons is not known, because the remaining 98 cocoons were destroyed by some unidentified predator at about the same time that the woodpecker attacks began.

The injury left by this unidentified predator(s) resembles neither woodpecker injury (Waldbauer et al., 1970) nor mouse (*Peromyscus* spp.) injury (Scarbrough et al., 1972). (As judged by the injury, all attacks on cocoons in the urban area had been by woodpeckers.) The holes in most of the cocoons attacked by unidentified predators were nearly 2 cm long and 0.5 cm wide. A few had long narrow slits 3 to 4 cm long. Most of these cocoons had been ripped open rather than chewed, abraded, or punctured. Sometimes, loose silk remained on them, but it had been pulled outward rather than pushed inward as is the case with woodpecker attacks. The entire pupa had been removed from each of these 98 cocoons—apparently in one piece, because the cocoons were not stained by the semi-liquid pupal contents that would have leaked out if the pupae had been pierced or broken into pieces. This seems to eliminate birds from consideration, since it is difficult to see how they could remove a large pupa through such a small hole without breaking it or at least piercing it.

The animal(s) most likely to be responsible are the fox squirrel, *Sciurus niger* L., gray squirrel, *S. carolinensis* Gmelin, and flying squirrel, *Glaucomys volans* (L.). They could rip the cocoons open with their incisors and remove the pupae with their front paws. According to Martin et al. (1951), gray squirrels eat pupae from unspecified cocoons and fox squirrels eat Lepidoptera of all stages. Both gray and flying squirrels are absent from Trelease Woods, but fox squirrels occur at both Trelease and Hart Woods (Lonnie Hansen, Illinois Natural History Survey, Urbana 61801, personal communication). Both fox and gray squirrels occur in Champaign and Urbana, but we have not found cocoons that bear this type of injury in the urban area. However, squirrels are almost confined to old or intermediate residential areas where cecropia cocoons are relatively scarce.

The cocoons taped to the bases of woody plants at Trelease and Hart Woods were almost ignored by mice, and none were attacked by other predators; two were opened by mice at Trelease and none at Hart Woods. On the other hand, similarly treated cocoons placed in rural areas where cecropia cocoons occur naturally were heavily attacked. Mice opened 65% of those taped to willows at Mayview and 40% of those taped to dogwood shrubs along Interstate 74. *Peromyscus leucopus* occurs both in the woods and in these other areas. We believe that woodland *P. leucopus* seldom attacked the taped cocoons,

because, like woodland woodpeckers, they had had no previous experience with cecropia cocoons. This view is supported by the finding of Scarbrough et al. (1972) that, in the laboratory, *P. leucopus* that had been trapped at a site where cecropia cocoons were abundant attacked and opened cecropia cocoons much more readily than did *P. leucopus* that had been trapped at Trelease Woods.

Each year we find in the urban area several dozen cocoons with various kinds of seeds, sometimes whole acorns, stuffed into their valves. We do not know how frequently this causes mortality, but on at least one occasion it blocked the emergence of an adult, causing its death. The responsible animal has not been identified, but it is probably the blue jay, *Cyanocitta cristata* L. (Waldbauer & Sternburg, 1976).

DISCUSSION

The local distribution of cecropia described above raises three obvious questions: 1) Why are they abundant in some urban environments and scarce in rural environments? 2) Why, in rural areas, are they virtually absent from forests but present, although in small numbers, in short trackside and roadside woody vegetation? 3) Why are they abundant in new urban residential areas but very scarce in old urban residential areas?

Old urban residential areas and forests both have characteristics of a climax, at least in that their woody vegetation consists largely of mature trees and shrubs. On the other hand, new urban residential areas and stands of small willows and other woody plants along railroad tracks and roads resemble an early stage in the succession. Thus, the fundamental question may be why cecropia is more abundant in early stages of the succession than in the climax. We have found what we believe to be a major reason for the difference in numbers of cecropia in urban and rural areas, but our discussion of the remaining questions is based largely on circumstantial evidence.

No doubt, a complex of factors is responsible for the greater abundance of cecropia in new urban areas than in rural areas (Table 1), but so far we have concrete evidence of only one such factor, a large difference in the predation pressure on the pupae in winter. In rural areas only about 29% of the overwintering pupae survived, but in the urban area about 66% of them survived (Waldbauer & Sternburg, 1967a; Scarbrough, 1970; Scarbrough et al., 1977). In both urban and rural areas, at least 90% of the pupae in cocoons that were exposed above the ground litter were killed by woodpeckers; this comes to about 6% of the pupae in the trackside vegetation at Mayview and about 20% of those in the urban area. However, in rural areas cocoons

spun near the ground (usually over 90%) are heavily attacked by mice, while cocoons spun near ground level in urban areas (about 80%) are virtually exempt from attack of any kind. During two winters at May-view, at least 62% of all cecropia cocoons were destroyed by mice, while in the urban area we have seen only three cocoons that were destroyed by mice out of several thousand that we have collected since 1965 (Waldbauer & Sternburg, 1967a; Waldbauer et al., 1970; Scarbrough et al., 1972). This 62% mortality includes cocoons that were opened where they had been spun (57.1%), plus others that were removed from the spinning site (4.8%). There is no doubt that the cocoons *in situ* had been opened by *Peromyscus* spp. (Scarbrough et al., 1972), and the removal of cocoons can probably also be attrib-uted to *Peromyscus* spp. Four cecropia cocoons and a *Peromyscus* nest were found next to each other under a log near Urbana; three of these cocoons had been opened (they bore the characteristic mouse injury), and one still contained a pupa (personal communication from Lloyd Davis, Dept. of Entomology and Nematology, University of Florida, Gainesville 32611). It may well be that considerably more than 62% of the cocoons at Mayview were destroyed by mice; we probably did not account for more than a few of the cocoons that had been removed, because the scraps of silk that are left behind are very difficult to find.

The reason for this striking difference in predation pressure is a difference in the feeding behavior of the species of mice that inhabit rural and urban areas. Extensive trapping showed that the native wild mice *Peromyscus leucopus* and *P. maniculatus* are almost absent from both new and old urban residential areas, but that the house mouse, *Mus musculus* L., is common there, constituting over 91% of the small mammals trapped on front lawns. In the urban area we caught *Pero-myscus* spp. only near stream banks or other intrusions of rural hab-itat. In rural areas the situation was reversed; over 89% of the small mammals caught were *Peromyscus* spp., but only 7.4% were *M. mus-culus*. In the laboratory *M. musculus* ate naked cecropia pupae and incorporated silk from the cocoons in their nests, but under no cir-cumstances did they open a cocoon to obtain a pupa. On the other hand, in the laboratory all *P. leucopus* and most *P. maniculatus* readi-ly opened cecropia cocoons and ate the pupae (Scarbrough et al., 1972).

We have less information on why cecropia is over thirteen times more abundant in new urban residential areas than in old urban res-idential areas (Table 3). It is very likely that cecropia follows a pattern that evolved long before Europeans came to the New World and built urban areas—that it is a "fugitive species" (Hutchinson, 1951) whose

population is constantly shifting to areas early in the succession. This is borne out by our observations over the past fifteen years. From 1965 to 1980 there has been a major shift in the location of the cecropia population in Champaign and Urbana. Residential areas that were new in 1965 now have much larger trees and produce very few cecropia cocoons, but other areas that were crop fields in 1965 have since become new residential areas that now produce many cocoons. Cecropia thus does seem to be a fugitive species that constantly "flees" to areas early in the urban succession. This pattern of scarcity in climax communities also seems to hold true in rural areas; as we saw above, cecropia was almost absent from woodlands, but occurred in small numbers in the early successional communities found along roads and railroad tracks (Table 1). We do find occasional cecropia larvae in the woodlands, but we have found only one cocoon there. Obviously, some oviposition occurs in the woodlands, but cecropia does not often survive past the larval stage there, suggesting that the population differences between early and late successional stages might be due to mortality that occurs before the pupal stage, probably in the larval stage.

Although we label cecropia a fugitive species, there still remains the question of what there is about the woodland climax or the "urban climax" that causes the cecropia population to be so low there. A lack of suitable food plant species cannot be responsible, because the same species of woody plants are about equally abundant in new and old urban areas (Table 5), and because the rural woodlands, tracksides and roadsides all have plant species that are often used as hosts by wild cecropia in this area. Woodlands and old urban areas might be discriminated against because of some direct response of cecropia to the size of the trees. For example, the females might prefer to oviposit on small trees. Another, and perhaps more likely, possibility is that cecropia are less likely to survive in woodlands and old urban residential areas because of a higher rate of predation and/or parasitization on the larvae.

We do have circumstantial evidence which suggests that predation by birds on the larvae may be a major reason for the paucity of overwintering cecropia in old residential areas. The new areas, built on former crop fields and lacking large woody plants, have a bird fauna that is very different from that of the old areas with their large trees and shrubs. Our own observations leave no doubt that ground-frequenting birds are common in the new areas. However, birds that search woody plants for caterpillars, although abundant in old areas, are relatively scarce in new areas. These are blue jays, brown thrashers (*Toxostoma rufum*), catbirds (*Dumetella carolinensis*), mockingbirds (*Mimus polyglottos*) and cardinals (*Richmondena cardinalis*).

We have seen all of these species prey on cecropia caterpillars in the field. Graber & Graber (1963) list all of the above mentioned species, except the mockingbird, as common residents of urban residential areas of central Illinois. However, we have seen mockingbirds in old residential areas of Champaign and Urbana on many occasions. Graber & Graber (1963) do not specify whether their data apply to old or new residential areas, but R. R. Graber (Illinois Natural History Survey, Urbana 61801, personal communication) told us that their data came almost entirely from old residential areas and that mockingbirds are common in old areas. The situation is similar in rural areas. Foliage-gleaning birds are abundant in the woodlands, especially at the edges where cecropia food plants are most abundant, but these birds are very scarce in the trackside and roadside areas.

Cecropia is attacked by several parasitoids (Marsh, 1937), but they cannot be responsible for the observed differences in cecropia population size between rural and urban areas or between old and new urban areas. Until 1975 less than 1% of the cocoons from Champaign Co. contained parasitoids. In 1975 about 5% of the cecropia cocoons in one small area of the city of Champaign contained cocoons of *Enicospylus americanus* (Christ) (Hymenoptera: Ichneumonidae). This parasitoid was relatively common and widespread in Champaign and Urbana in 1979–80, but was very uncommon in 1980–81. We have found a few cocoons containing larvae that had apparently died of disease, but we know nothing of the incidence of death in younger larvae due either to disease or parasitism.

Cecropia must be highly mobile to locate early successional areas so rapidly. Nothing is known of how far the females fly, but it is known that the males are often caught from 6.8 to 12.5 km away from the release point in traps baited with virgin females (Sternburg & Waldbauer, J. Lepid. Soc., in press).

The list of cecropia's preferred food plants (Scarbrough et al., 1974 and references therein) supports the idea that cecropia is essentially a species of the early stages of succession. Included on this list are such early successional plants as the poplars (*Populus* spp.), willows (*Salix* spp.), thorn apples (*Crataegus* spp.), wild black cherry, staghorn sumac (*Rhus typhina* L.), silver maple, box elder maple and the birches (*Betula* spp.). Even in the urban environment 54.2% of the cocoons found on food plants were found on plants included on the preceding list.

LITERATURE CITED

DOWNING, E. R. 1921. A metrical study of a thousand moth cocoons. Trans. Ill. State Acad. Sci., 14:140–141.

FERGUSON, D. C. 1972. Bombycoidea (in part), pp. 246–259 *in* Dominick et al. (eds.). The moths of America north of Mexico. Fascicle 20.2B. Classey, London.

Graber, R. R. & J. W. Graber. 1963. A comparative study of bird populations in Illinois, 1906–1909 and 1956–1958. Ill. Nat. Hist. Surv. Bull., 28:383–528.

Hutchinson, G. E. 1951. Copepodology for the ornithologist. Ecology, 32:571–577.

Marsh, F. L. 1937. Ecological observations upon the enemies of *cecropia* with particular reference to its hymenopterous parasites. Ecology, 18:106–112.

Martin, A. C., H. S. Zim & A. L. Nelson. 1951. American Wildlife and Plants, a Guide to Wildlife Food Habits. Dover, New York, 500 pp.

Maughan, J. 1906. Cecropia emperor moth. Ottawa Nat., 20:180–190.

Miller, A. E. 1927. Oddities in cocoons of some common Saturniidae. Ent. News, 38:11–13.

Porter, G. S. 1912. Moths of the Limberlost. Doubleday, Page & Co., Garden City, New York, 370 pp.

Rau, P. & N. Rau. 1914. Longevity in saturniid moths and its relation to the function of reproduction. Trans. Acad. Sci. Saint Louis, Mo., 23:1–78.

Scarbrough, A. G. 1970. The occurrence of *Hyalophora cecropia* (L.) as related to urbanization. Ph.D. thesis, University of Illinois, Urbana, IL, 212 pp.

———, J. G. Sternburg & G. P. Waldbauer. 1977. Selection of the cocoon spinning site by larvae of *Hyalophora cecropia* (Saturniidae). J. Lepid. Soc., 31:153–166.

———, G. P. Waldbauer & J. G. Sternburg. 1972. Response to cecropia cocoons of *Mus musculus* and two species of *Peromyscus*. Oecologia, 10:137–144.

——— 1974. Feeding and survival of cecropia (Saturniidae) larvae on various plant species. J. Lepid. Soc., 28:212–219.

Smith, J. B. 1899. Insects of New Jersey. 27th Ann. Rept. State Board of Agric., 27:25.

——— 1908. Notes on some cecropia cocoons and parasites. J. Econ. Ent., 1:293–297.

Smith, M. C. 1957. Historical geography of Champaign County, Illinois. Ph.D. thesis, University of Illinois, Urbana, IL, 125 pp.

Sternburg, J. G. & G. P. Waldbauer. 1969. Bimodal emergence of adult cecropia moths under natural conditions. Ann. Entomol. Soc. Amer., 62:1422–1429.

Sweadner, W. R. 1937. Hybridization and the phylogeny of the genus *Platysamia*. Ann. Carnegie Museum, 25:163–242.

Thompson, W. R. R. & W. F. Fiske. 1909. Notes on the parasites of Saturniidae. J. Econ. Ent., 2:450–460.

Waldbauer, G. P. 1978. Phenological adaptation and the polymodal emergence patterns of insects, pp. 127–144 *in* H. Dingle (ed.). The Evolution of Insect Migration and Diapause. Springer-Verlag, New York.

——— & J. G. Sternburg. 1967a. Differential predation on cocoons of *Hyalophora cecropia* (Lepidoptera: Saturniidae) spun on shrubs and trees. Ecology, 48:312–315.

——— 1967b. Host plants and the locations of the baggy and compact cocoons of *Hyalophora cecropia* (Lepidoptera: Saturniidae). Ann. Entomol. Soc. Amer., 60:97–101.

——— 1973. Polymorphic termination of diapause by cecropia: genetic and geographic aspects. Biol. Bull., 145:627–641.

——— 1976. Emergence of *Hyalophora cecropia* (Saturniidae) blocked by seeds in the cocoon valve. J. Lepid. Soc., 30:131–132.

Waldbauer, G. P., J. G. Sternburg, W. G. George & A. G. Scarbrough. 1970. Hairy and downy woodpecker attacks on cocoons of urban *Hyalophora cecropia* and other saturniids (Lepidoptera). Ann. Entomol. Soc. Amer., 63:1366–1369.

GENERAL NOTES

A. S. PACKARD ON A FORMER CONNECTION BETWEEN BRAZIL AND AFRICA BASED UPON HIS STUDY OF LEPIDOPTERA

At the 8th International Geographical Congress held in 1904 at St. Louis, Missouri, Dr. A. S. Packard, Jr. (1839–1905) read a paper entitled "Evidence in favor of the former connection of Brazil and Africa and of an originally Antarctogaeic land mass." Packard had been one of the founding curators of the Peabody Academy of Science at Salem, Massachusetts, and for a few years served as its director before going to Brown University as professor of zoology and geology. While at Salem he was also one of the founders of the *American Naturalist,* which he served for many years as the chief editor. He was primarily an entomologist specializing in the Lepidoptera, about which he published many articles and monographs. He also published on a wide variety of entomological and zoological topics, on glacial geology, and produced many textbooks on entomology and zoology. (See Remington, 1947, Lepid. News, 1(4):39; Dexter, 1956, Amer. Nat., 90:209–225; 1957, Bull. Brooklyn Entomol. Soc., 52:57–66, 101–112; 1981, Bios, 52(1):4–7.).

Packard's paper delivered at the Congress was published the following year (1905, Rept. 8th Internat. Geograph. Cong. (1904), 638–640). In this he stated that, based on his studies on the distribution of Lepidoptera, "we should not be too much influenced by the hypothesis or dictum of the permanency of the ocean basins" (p. 640). He offered, "a theory of a former land connection between Brazil and West Africa along or near the equator" (p. 638). From data he accumulated on South American and African species of Lepidoptera, he pointed out that "An extensive group of large African moths (Bunaeinae) are nearest allied to the Neogaeic group Ceratocampidae; still stronger resemblances exist between a Chilean genus of another group, and an African subfamily (Urotinae). Another large and important family (Hemileucidae), now chiefly confined to South and Central America (Neogaea), has representatives in the Ethiopian realm. Within this group are several highly specialized genera which occur in tropical and southern Africa. There are in short, five groups of South American Syssphrigine moths alone which have representatives in Western or Southern Africa, the latter so highly specialized as to suggest their primitive origin from Neogaea. Several groups of butterflies also afford parallel facts" (p. 639).

To explain these inter-continental distributions Packard then hypothesized, "It thus appears that it would require an elevation of the ocean bottom of from about one to two miles between Brazil and Sierra Leone, Africa, to form a more or less continuous land connection between the two continents apparently sufficient to account for the spread or intermigrations in pre-Miocene times of plants and animals between what are now two widely separated areas" (p. 640).

Ortmann (1901, Amer. Nat., 35:139–142) had reviewed in general the literature on the theory of land connections in the southern hemisphere, and was convinced that southern land masses had been connected in past geologic time. The following year (Ortmann, 1902, Proc. Amer. Philos. Soc., 41:267–400) he amassed data to substantiate the theory, and added the results of his own research on freshwater crustaceans. Then Packard presented his evidence based on insect distribution and gave his explanation as we have seen above.

Eight years after Packard's paper was presented, Alfred L. Wegener (1880–1930) published (1912, Geologische Rundschau, 3(4):276–296) his now famous and generally accepted theory of Continental Drift. This work was expanded, and an English edition entitled "The origin of continents and oceans" was published in 1924 (Methuen, London, 212 pp.). Today biogeographers would favor Wegener's theory over that of Packard. However, it is interesting to note that Packard at an early date recognized a former connection between South America and Africa based upon the distribution of certain species of Lepidoptera.

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THE PIERID FAUNA OF JEWEL FLOWER AT A
MID-ELEVATION SIERRAN LOCALITY

Jewel flower (*Streptanthus tortuosus* Kell.) is one of the commonest, most wide-spread native Californian crucifers. Unlike many other *Streptanthus*, it occurs over a wide altitudinal range and on many different soils. Recent studies of endemic serpentine-barren *Streptanthus* in the North Coast Ranges have shown that 50% or more of the plants may receive pierid eggs, and larval damage may affect from 15% to 40%, depending on species, phenophase, and site (Shapiro, Amer. Nat., 117:276–294; Shapiro, unpublished). In these low-diversity communities three pierids (*Pieris sisymbrii* Bdv., *Anthocharis sara* Lucas, and *Euchloe hyantis* W. H. Edw.) feed more or less synchronously on two *Streptanthus* (*breweri* Gray, *glandulosus* Hook. vars.), which are both among the commonest herbaceous species. One larva of *P. sisymbrii,* surviving to pupation, can destroy the entire seed output of one medium-sized or several small *Streptanthus* plants.

At higher elevations the crucifer-feeding pierid fauna is more complex. On 25 June 1980 a census of pierid immatures was carried out on *S. tortuosus* along the Bowman Lake Road above Lang Crossing of the South Yuba River, Nevada Co., California, on the west slope of the Sierra (1400–1500 m). The site is a steep, xeric, sparsely vegetated slope (scattered montane chaparral on a quartz-muscovite-biotite-feldspathic schist). The aspect of the site is open and similar to a serpentine barren. *S. tortuosus* is an aspect dominant in the herb layer. The only other crucifers present are three species of *Arabis*, all rare (two known from one clump each on the slope), and the weed *Lepidium virginicum* var. *pubescens* (Greene) Thell. of which a few examples were found by the roadside. Most of the *Streptanthus* grow on ledges; their distribution is highly clumped. The crucifer-feeding pierid fauna of the general area includes nine species (four Euchloini, five Pierini); of these five are regular residents of the site (*Anthocharis sara, A. lanceolata* Lucas, *Euchloe hyantis, E. ausonides* Lucas, and *Pieris sisymbrii*) and a sixth (*Pieris rapae* L.) occurs as a stray.

One thousand, nine hundred and twenty-five *S. tortuosus* were examined. They had green fruit, and most still had a few flowers. Of the pierid species, *E. hyantis* (one seen) and *P. rapae* were still flying locally. Some 236 plants had been damaged in a characteristic pierid manner ("stemmed"): 43 larvae were found: 28 *E. hyantis* (2nd instar through prepupa), 7 *A. lanceolata* (2nd through 4th instars), 5 *A. sara* (3rd through 5th), 2 *P. sisymbrii* (one each, 4th and 5th), and 1 *P. rapae* (5th instar). All of these are obligate or preferential silique feeders, except *P. rapae*. No pierid eggs were found. Injury ranged from minor (by small larvae working the distal portions of single stems) to major and even complete (Fig. 1). Total plants damaged equaled 12.3%, with the average damage on these plants as of the sampling date being a 20% loss of siliques. Thus, by 25 June about 2½% of the reproductive potential of the plant population had been lost to pierid feeding. Shapiro (1975, Amer. Midl. Nat., 93: 424–431) estimated the seed loss of *Lepidium virginicum* to pierids at Donner Pass as about 1.4%. Both figures are substantially lower than on serpentine in the Coast Range. The extent of further depredation at Lang Crossing can be guessed at, noting that most of the small larvae of both *E. hyantis* and *A. lanceolata* collected June 25 were parasitized and were killed by an undetermined hymenopteran within four days from collection, with little further feeding. The bulk of the season's damage had presumably already been inflicted.

There is no general agreement among ecologists as to the criteria for recognizing either interspecific competition or food limitation on population growth in herbivorous insects, which rarely devastate their hosts in a state of nature. The leading authority on *Streptanthus*, A. R. Kruckeberg, writes (in litt.): "Having collected members of the genus ever since 1948, you should think I would have discovered instances of insect predation, yet I rarely do find them . . . in good years climatically, I can find an abundance of seed with inflorescences loaded with siliques up to the aborted terminal flowers of the raceme." Yet some of the serpentine *Streptanthus* appear to have evolved specific anti-herbivory mechanisms directed at pierids (Shapiro, Amer. Nat., *loc. cit.*).
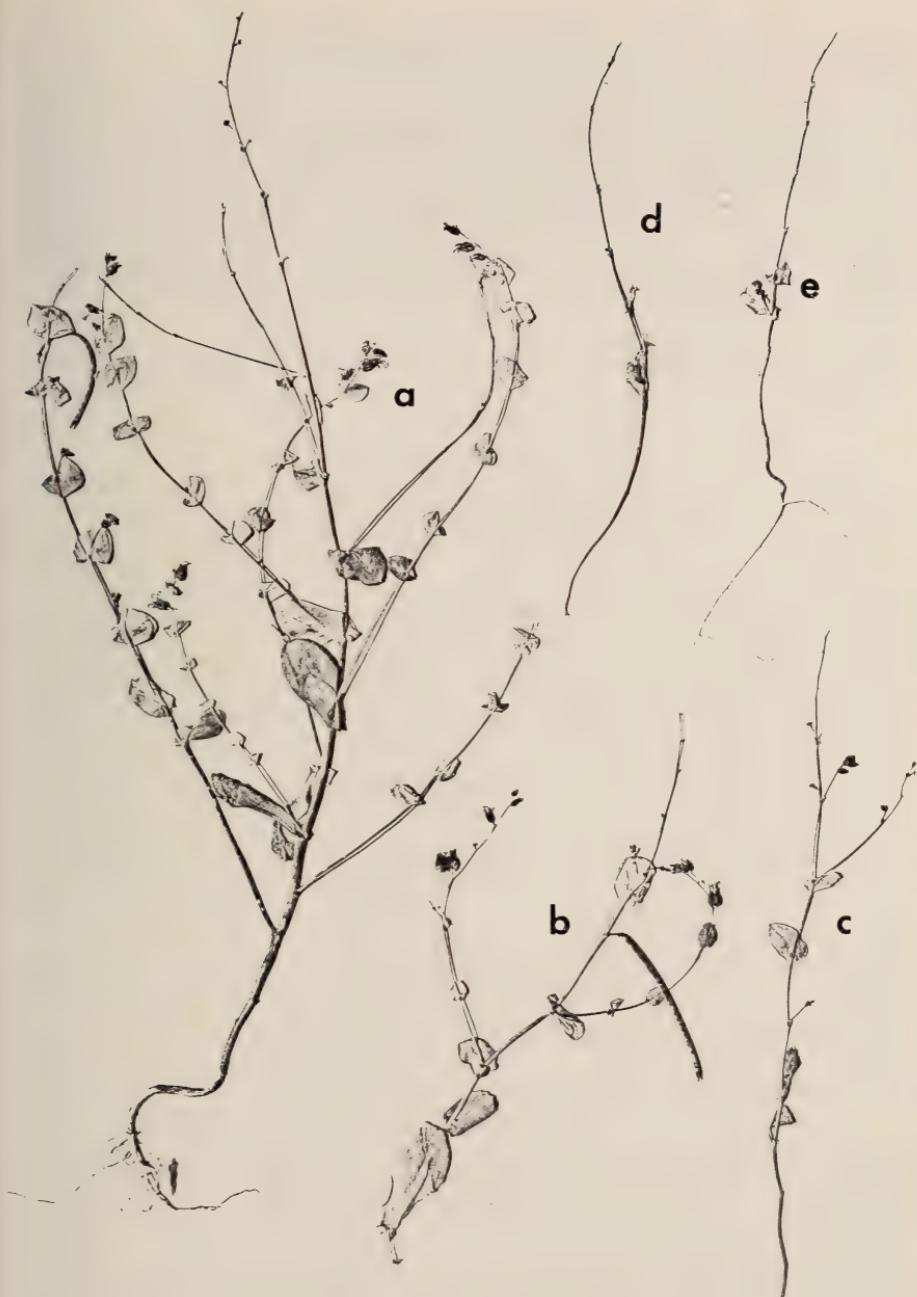
FIG. 1. *S. tortuosus* collected at Lang Crossing, vi.25.80, showing feeding damage inflicted by *Euchloe hyantis* (larvae collected from all specimens). **a:** destruction of almost all siliques by one mature larva. This large, vigorous plant had the potential to produce a second seed crop before the end of the growth season. **b:** medium-sized plant with most of inflorescence destroyed by a third-instar larva. **c:** small plant with all siliques destroyed by third-instar larva, but a few flower buds intact. **d, e:** small plants with all siliques destroyed; these individuals had no prospect of recovery.

The impact of pierid feeding must be assessed the level of the individual plant rather than the population as a whole; then it can be seen that a single oviposition can be effectively lethal. If larval survivorship is high, most plants that receive one pierid egg will fail to set seed. If it is lower, the losses will be less, but still may be substantial. In *S. tortuosus* at Lang as with other crucifers (Shapiro, loc. cit.) the brunt of injury is borne by peripheral and isolated individuals rather than those in large stands; pierids consistently disobey the "resource concentration hypothesis" (Root, 1973, Ecol. Monogr., 43: 95–124). Since other herbivores, including the flea beetles *Phyllotreta* (Chrysomelidae), are density-dependent, *Streptanthus* may be under conflicting selection pressures affecting spacing or seed dispersal. The relatively low overall impact of pierids on seed production at Lang may reflect the highly aggregated dispersion of the plants, since attack is so catastrophic to the victims.

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FIELD NOTES ON FOUR WESTERN HAIRSTREAKS
(LYCAENIDAE: THECLINAE)[1]

Many collectors tend to overlook or ignore some of the hairstreaks found in the Rocky Mts. Those that avidly seek nectar at flowers are conspicuous and are collected with some frequency. These include such species as *Strymon melinus* Hübner, *Mitoura siva* (W. H. Edwards), *Harkenclenus titus* (Fabricius), and *Callipsyche behrii* (W. H. Edwards). Other species generally perch on their larval host plants, usually shrubs or scrub trees, and do not visit flowers on a regular basis; although sometimes they may be taken in numbers at flowers. Four such species are the subject of this paper.

I will discuss the habits and habitats of some of the more elusive hairstreaks found in the western United States. Some species that are considered rare are probably relatively common, but occur only in narrowly-defined biogeographic areas. In addition, their habit of not straying very far from their larval hosts affords an additional measure of protection from the casual butterfly collector.

Some taxonomic matters are discussed, but no actions are taken in this regard.

Satyrium calanus Hübner, 1809

Western populations of *S. calanus* are usually assigned to the subspecies *godarti* Field (1938a). In the Rocky Mt. region, there is considerable variation among populations of this insect. The usual form in some regions would be considered as highly aberrant in other portions of its range.

I discovered this species in Wyoming in 1977. Oak, the larval host, does not grow generally in Wyoming. *Quercus macrocarpa* Michx. is found in the Black Hills in the extreme NE part of the state; *Quercus gambelii* Nutt. occurs in an isolated colony on the western slope of the Sierra Madre in Carbon Co. The only specimens of *S. calanus* collected to date in Wyoming are the form shown in Fig. 1 from the Sierra Madre. The ventral surface varies from pale shades of gray to white. A similar form from Manitoba was named *heathii* by James Fletcher (1904, Can. Entomol., 36(5): 121–130). A. H. Clark (see Field, 1938, Bull. Univ. Kansas, 39(10): 1–328) later placed *heathii* as an aberrational form of *S. calanus falacer* (Godart). See Fisher (1976, J. Res. Lepid., 15(3): 177–181) for additional discussion of "heathii" forms. The white-banded aberrational or "heathii" form appears in several North American hairstreaks. In Carbon Co., Wyoming and Routt Co., Colorado (vic. Rabbit Ears Pass), it is the normal form. In several years of collecting this species in Wyoming, I have yet to take a specimen with the dark ventral markings typical of *godarti*.

It is not clear why the aberrational form is the rule in this geographic region. Soil chemistry might be a factor, as has been demonstrated for a few butterfly species (in litt.), although other hairstreaks that occur in the region do not exhibit such aberrations. *S. calanus* and *S. liparops aliparops* (Michener & dos Passos) fly together in Carbon Co., Wyoming. Another factor might be geographic isolation (a relict population as it were). It may be that, because of the host plant isolation over the millennia, the aberrational form has become genetically dominant for some reason. Since the "heathii" form occurs in other *calanus* populations, it does not seem wise at this time to describe the Carbon Co. phenotype as a new subspecies.

The Wyoming habitat is shown in Fig. 17. The area is a well-drained hillside with groves of trees and open meadows. The short dark trees are oaks; the trees with white bark are aspens. The butterflies perch on the oaks and occasionally may be taken on flowers.

Figs. 2–4 illustrate *godarti* from Union Co., New Mexico. No figures appear in Field's description of this subspecies. The two males and one female shown are from the same collection site. Note the wide variation in facies, especially in the VFW bands. These three specimens are typical of the variation found in a large series (over 60 specimens)
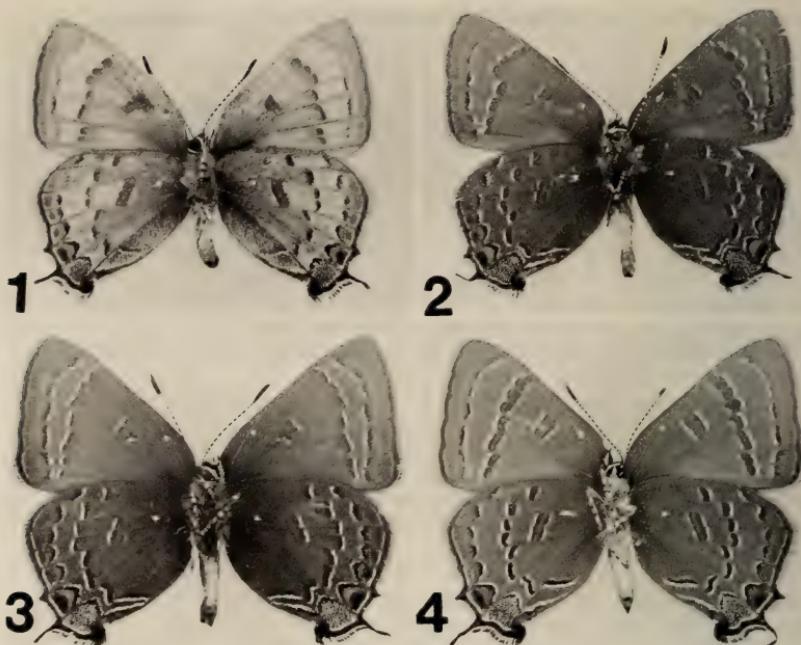
FIGS. 1–4. *Satyrium calanus godarti*: **1**, male V, Wyoming population, W. slope Sierra Madre Mts., Carbon Co., Wyo., 26-vii-78; **2, 3,** males V, Oak Creek, NE of Folsom, Union Co., New Mexico, 28, 29-vi-79; **4,** female V, same data.

taken at the same locality. They were collected in extreme NW Union Co., north of Folsom. This region is dotted by volcanic cones and there are periodic outcroppings of scrub oak. Additional collecting notes are included in the subsequent discussion of *Fixsenia ontario violae* (Stallings & Turner).

Fixsenia ontario violae (Stallings & Turner) (1947, Pan-Pac. Entomol., 23(3):119–120)

Emmel, in Howe (1975, The Butterflies of N. Amer., Doubleday & Co., New York) stated about *F. o. violae*: "This rare subspecies, known only from the type series, is . . . ." This butterfly is probably very local, but more common than Emmel's statement would lead one to believe. Figs. 5–8 illustrate this butterfly; Stallings & Turner did not do so. The type series of 24 specimens was collected at 5600′ (1708 m) along the Cimmaron River (fide M. S. Fisher), north of Folsom, Union Co., New Mexico. A series was collected along Oak Creek, NE of Folsom in June 1970 by R. E. Stanford and M. S. Fisher. They found adults sipping nectar from yellow sweetclover (*Melilotis officinalis* (L.) Lam.) that was growing along a highway (Stanford, in litt.). A few additional specimens were taken along the Colorado-New Mexico border just south of Branson, Colorado.

I collected along Oak Creek in late June 1979. Most of the sweetclover had been mowed. No *ontario* were to be seen, although several other hairstreaks, including *S. calanus godarti* were taken on the remaining sweetclover and a milkweed that was growing along the highway.

My small series of *violae* was taken over a two-day period by the traditional method of beating the scrub. It helps to have an extra net handle or a stout stick along for this purpose. One thrashes the shrubbery (scrub oak in this instance) and waits to see what
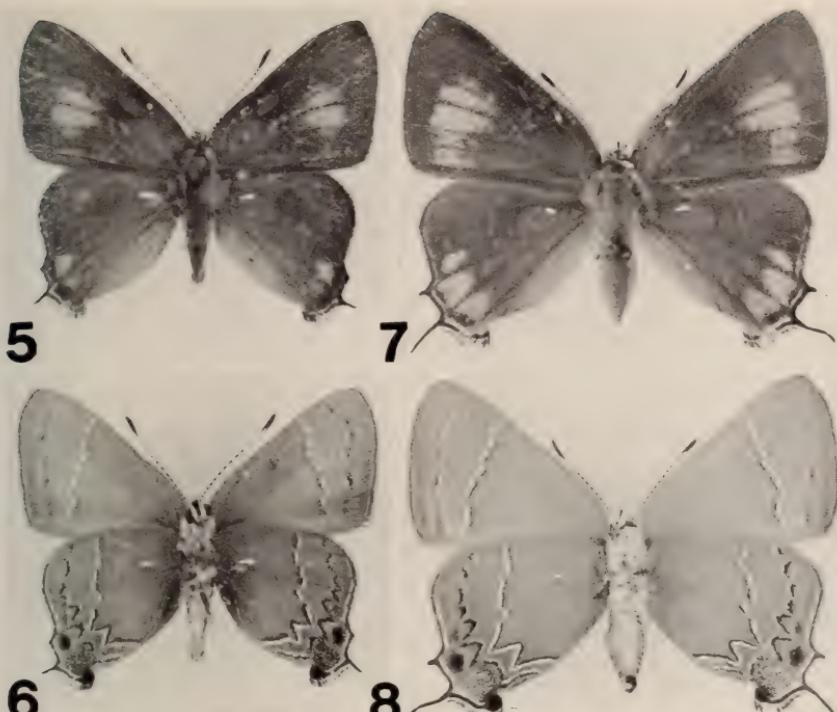
FIGS. 5–8. *Euristrymon ontario violae*: **5,** male D, Oak Creek, NE of Folsom, Union Co., New Mexico, 28, 29-vi-79; **6,** same V; **7,** female D, same data; **8,** female V.

flies out. My first attempts yielded nothing but leafhoppers; then a few *calanus godarti* were flushed. The next attempt was made on a ring of oaks encircling a large globular juniper. The oaks were about 8–10 feet tall. The first thrash produced a cloud of hairstreaks, a number of which were collected, all *godarti*. On the second thrash, one or two paler and slower flying hairstreaks were seen.

The *godarti* tended to settle and perch toward the tips of the oak branches, where they were quite visible. The others, which proved to be *violae*, settled deeper among the leaves and were more difficult to collect. Diligent and determined whacking of this one oak grove produced 39 *godarti* and 10 *violae*. By the time that these specimens had been collected, the sky was heavily overcast, the sun low in the west, and biting gnats were feasting on the collector.

Collecting the next morning, following a night of natural pyrotechnics, produced another 28 *godarti* and a few more *violae*. Although the sky was clear after the nocturnal thunderstorm, there was a stiff breeze and *violae* did not seem prone to fly, even with thorough thrashing of the scrub oak. Specimens were taken, however, from several different localities in the general area of Oak Creek.

I suspect that the rarity of this butterfly in collections relates both to method of collection, and the fact that the habitat is well off the beaten path for most collectors. I did not find it south of Branson. The elevation there is just slightly higher than the Oak Creek site (6300′ versus 6100′), and the butterflies had perhaps not yet emerged.

Phaeostrymon alcestis (W. H. Edwards) (1871, Trans. Amer. Entomol. Soc., 3: 266–277)

Maurice L. Howard of Pueblo, Colorado discovered this species in Cottonwood Canyon (Baca-Las Animas Co.), in extreme SE Colorado. The holotype of *P. a. alcestis* was collected in Dallas, Texas. In 1904 (J. N.Y. Entomol. Soc., 12: 39–44), Dyar described
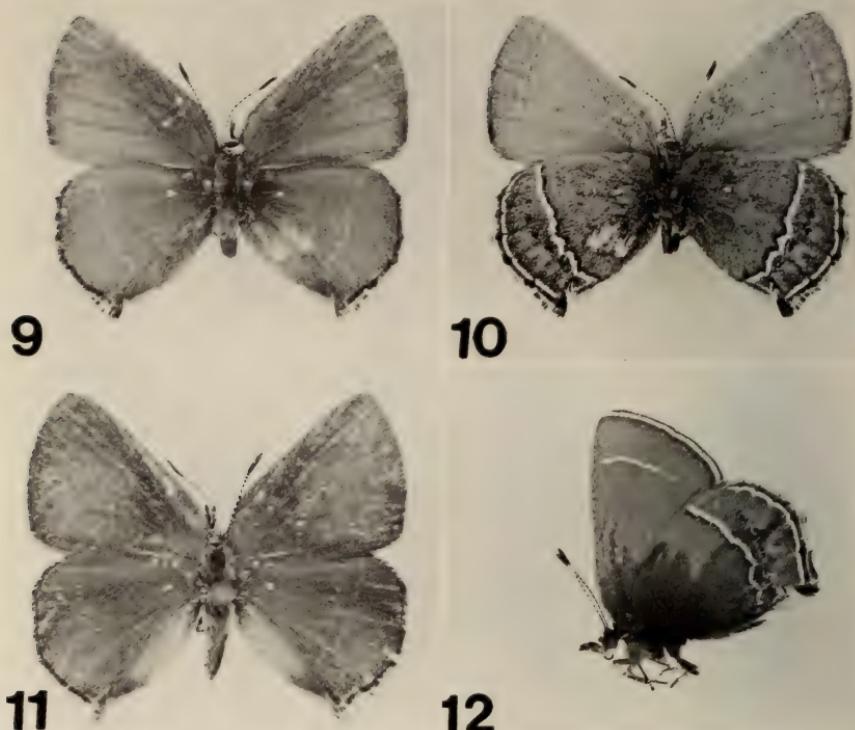
FIGS. 9–12. *Sandia macfarlandi*: **9**, male D, Rancho Campana Agric. Sta., Chih., Mexico, 9-iv-72, Leg: R. J. Lavigne; **10**, same V; **11**, female D, same; **12**, female V, same locality, 3-iv-72.

P. a. oslari from Tucson, Arizona. In his description of *oslari*, Dyar stated: "Closely allied to *alcestis* Edwards. It is smaller, a grayer brown on the upper side, ashen gray, not brown below and the red markings beyond the outer band are less developed." Generally speaking, Arizona and New Mexico specimens are much paler in all colors than *alcestis* from Texas and Kansas. There is very little color variation within given colonies of either subspecies (*sensu stricto*).

Material from Cottonwood Canyon, on the other hand, is extremely variable. A series collected in 1974 and sent to me by Prof. Howard, exhibits both the typical *alcestis* phenotype and the normal *oslari* phenotype. Most of the specimens are intermediate between these two extremes. This is the only intermediate colony known to me, although others may exist.

I have not collected *alcestis* in Cottonwood Canyon. The larval host in SW New Mexico is *Sapindus drummondi* Hook. & Arn. (western soapberry). The butterflies perch in the flower clusters, where they are very difficult to see. The trees are usually 15–20 feet tall, with the flower clusters at their tops. One must use a "tropics" net with an extension handle. I have found that the best collecting method is to throw a rock into the flower clusters and then watch for the butterflies. With luck, one can see where they settle and then sweep the area with the net. If a colony is located in juvenile *Sapindus*, the beating method for *F. ontario* can be used effectively.

Sandia macfarlandi Clench & Ehrlich (1960, Ent. News, 71: 137–141)

This butterfly was originally described from Bernalillo Co., New Mexico. The original description mentioned two specimens taken by J. M. and S. N. Burns in the Davis
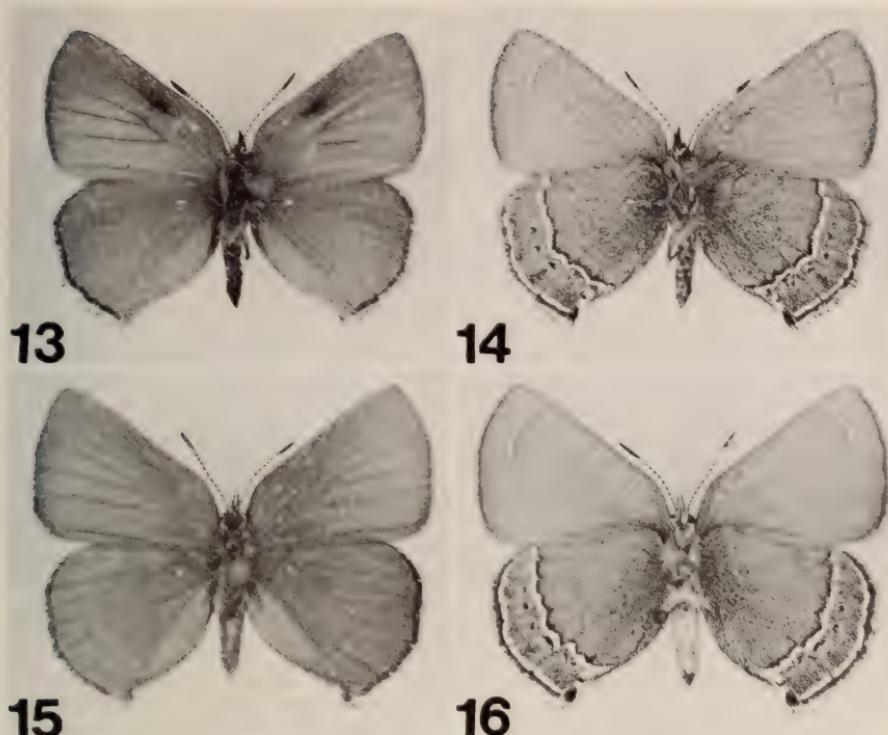
FIGS. 13–16. *Sandia macfarlandi*: **13,** male D, La Cueva Can., Bernalillo Co., New Mexico, 4-vi-79; **14,** same V; **15,** female D, same; **16,** same V.

Mts., Jeff Davis Co., Texas. Through the efforts of several itinerant and resident New Mexico collectors, this species is now recorded from eight or more counties in New Mexico.

In 1972 a colleague of mine at the University of Wyoming, Dr. Robert J. Lavigne, visited the Rancho Campana Agricultural Station, located about 100 km north of Chihuahua City, Chih., Mexico. He was studying Asilidae (robber flies) and collected one with a lycaenid prey. He then collected several more of the butterflies for reference. They were given to me to identify, and I confirmed their identity as *Sandia macfarlandi*. Three of the nine specimens collected are shown in Figs. 9–12. Topotypical specimens are shown in Figs. 13–16.

Although there are some slight differences in facies between the Mexican and New Mexican material, they are not considered sufficient to erect a new subspecies. Dorsally the males from both areas are similar; the Mexican females are a warmer and darker brown than typical New Mexico specimens. Ventrally, there are two slight differences. The Mexican specimens manifest a more yellow-green ground color than appears in topotypical specimens. In New Mexican *macfarlandi* the dark row of spots just distad of the post discal band (VHW) follows the contour of the band. In Mexican specimens, this spot row tends to diverge slightly as it approaches the HW costa.

The male and female genitalia have been studied for both populations. No differences have been detected on a geographic basis. The shape of the signa in the female bursae of both populations is identical.

The habitats of the two populations are quite similar. Figs. 18–19 illustrate the habitat at Rancho Campana. Clumps of *Nolina texana* Wats., the larval host of *Sandia*, can be

FIGS. 17–20. **17,** Habitat of *S. calanus* and *S. liparops* in Sierra Madre Mts., Carbon Co., Wyo. **18, 19,** Habitat of *S. macfarlandi* at Rancho Campana, Chih., Mexico. **20,** Robber fly with *S. macfarlandi* as prey at Rancho Campana.

seen in the foreground of both scenes. The terrain around La Cueva Canyon, the type locality of *S. macfarlandi,* in the foothills of the Sandia Mts. looks very similar to the Mexican habitat.

Fig. 20 shows a robber fly, *Efferia triton* (Osten-Sacken) wtih *S. macfarlandi* as prey. The butterfly, now in the author's collection, is illustrated in Fig. 12 also.

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BOOK REVIEWS

THE MOTHS AND BUTTERFLIES OF GREAT BRITAIN AND IRELAND, Volume 9, Sphingidae-Noctuidae (Part 1), edited by John Heath, A. Maitland Emmet, et al., 1979. Curwen Books, North Street, Plaistow, London E13 9HJ, England. 288 pp., 16 plates. £25.00.

This 20 × 25 cm volume is the second to be published in a projected series of 11, of which the last will be devoted to larvae. Volume 1, containing the introduction and section on primitive microlepidoptera, with four colored and nine monochrome plates, appeared in 1976. Volume 9 has eight contributing authors and covers the Sphingidae (W. L. R. E. Gilchrist), Notodontidae, Lymantriidae, Arctiidae (C. G. M. de Worms), Thaumetopoeidae, Ctenuchidae (J. Heath), Nolidae (R. J. Revell), and the first two subfamilies (Noctuinae and Hadeninae) of the Noctuidae (R. F. Bretherton, B. Goater, & R. I. Lorimer). It begins with an illustrated, 8-page chapter on eversible structures by M. C. Birch. Treatment of each species generally follows the sequence of scientific name, common name, synonymy, type-locality, description of imago, similar species, life history, distribution (with map), and with sections on occurrence and distribution or economic importance sometimes added. A special effort seems to have been made to include all significant food-plant information. The fine distribution maps for almost every species will have particular appeal to British lepidopterists.

It is difficult to avoid making comparisons between this work and its North American counterpart, *The Moths of America North of Mexico*. Both are products of the Curwen Press, are written by various specialist authors, and they fulfill comparable roles, i.e., to provide comprehensive, authoritative, faunal reference works for their respective regions, with keys where appropriate and every species illustrated in color. The British work is illustrated mainly with colored drawings by Brian Hargreaves, rather than by photography. It of course deals with a much smaller fauna, and its information content is in some ways less comprehensive. For example, some synonymic names are listed, with references, but synonymies are not complete, especially for genera. Type-localities are given only for the species or subspecies names accepted as having priority, not for junior synonyms. Structural features, such as genitalia and wing venation, are illustrated sparingly, but on the other hand the book does have three introductory colored plates (38 photographs) of live moths and larvae. In order to cover an inadequately known fauna, the American series must present results of new research, including original descriptions, revised classifications, and synonymies in the unabbreviated style of taxonomic revisions, while trying to appeal to both amateur and professional. Distribution maps have been omitted. The British series does not have to depend heavily on original research, because that fauna is relatively well known.

The brief generic treatments by the different authors of the British work are uneven, as mentioned in the editors' preface, and major diagnostic group characters are often not mentioned. Although the book begins with a special section on eversible structures (scent organs), this refers to adults only. Neither here nor on turning to the part on Lymantriidae did I find any mention of the dorsal abdominal glands by which lymantriid larvae are most easily recognized. The 13 plates of adult moths at the end of the book are quite good and better than those of Volume 1, but some plates seem to be deficient in red. Also, the wing patterns have a somewhat sketchy, harshly contrasting quality that is not typical of Hargreaves' work. I do not understand the reason for this. The plates of Volume 1, if anything, are low in contrast, and perhaps it was to correct this that the printer switched to a heavier, smoother paper for Volume 9.

This series is particularly well designed for the well-informed, non-professional audience, namely Britain's large population of amateur entomologists and naturalists, but it will undoubtedly serve as the standard reference work on British Lepidoptera for amateurs and professionals alike, in Britain and around the world, offering an alternative to Richard South's *The Moths of the British Isles*, which has been in general use for about 70 years. The editors and authors of this publication venture are to be congratulated.

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BUTTERFLIES OF THE AFROTROPICAL REGION, by Bernard d'Abrera. 1980. Large 4to, 593 pp., illustrated throughout in color. Lansdowne (Melbourne), in association with E. W. Classey. Price in the U.K. £59.50.

Having been so closely involved with the genesis of this book, it is not easy for me to be entirely detached in reviewing it. Nevertheless, d'Abrera has said so little about the relationship of his work to mine, other than the initial statement on the title page, that I feel I must enlarge upon it, lest I be held responsible for the shortcomings of his book.

The catalogue mentioned by d'Abrera is the unpublished first draft of an annotated checklist of the African butterflies (including the Hesperiidae, not covered by him). This will, in due course, be published by the British Museum (Natural History) after being checked, further elaborated upon, and revised where necessary by members of the staff of that institution. It includes a complete synonymy with references to the literature for all names and type localities, as well as a full bibliography and much detailed information on range and habitat.

In his text d'Abrera has made little attempt to distinguish his own taxonomic innovations from mine, and I must therefore take this opportunity to disclaim responsibility for at least two of his worst errors: Page 310: d'Abrera has raised *E. (B.) mardania dealbata* to specific rank on grounds which are clearly invalid. If he considers the eastern populations to be specifically distinct from those of central and western Africa, *orientis* Karsch, 1895, is the oldest available name, not *dealbata* Carcasson 1958. Page 358: d'Abrera has revived the specific status of *C. epijasius* Reiche, but not that of *C. saturnus* Butler. These two taxa may not be conspecific, but if so, it is absurd to separate *jasius* L. from *epijasius* but not from *saturnus*.

Apart from these somewhat personal comments, d'Abrera's book suffers from three major weaknesses. It was put together in great haste, the format and layout do not lend themselves to a work of such size, and the plates leave a good deal to be desired. In a field guide it is useful to have the figures accompanying the text for easy identification, but this is not necessary in a large book of this sort. Indeed, in d'Abrera's book this format has resulted in large areas of blank paper and wasted space in the plates, despite a seriously undernourished text. The book lacks an introductory discussion, vegetation maps, any mention of the biogeographic divisions of the African butterfly fauna, and it contains no consideration of how this fauna relates to that of other faunistic regions. Within the text there are no references to the literature, and the year of publication is given only for specific names. Brackets denoting generic substitutions have not been used, making it difficult to trace original descriptions. There is only a mention of species and subspecies, which have not been figured. There are no generic diagnoses, and family descriptions are sketchy in the extreme. Subfamily and tribal names have been ignored, even for the endemic Lipteninae, which are such a characteristic feature of the African fauna. There is no mention of early stages or larval food-plants.

Many of the specimens illustrated are old, worn and torn, and the method of pinning them on a light background and using flash seems especially designed to emphasize every imperfection. Many of the species which are illustrated with very poor specimens, or not at all, are represented by long fresh series in the National Museum of Nairobi. Although d'Abrera visited Kenya, apparently he did not bother to make use of the museum collections. Reproduction of many plates is fuzzy, a number of captions have been transposed, and some of the specimens figured have been misidentified. There are many unaccountable omissions, misspelt names and localities, wrong naming authorities and inaccurate distribution data. In reading through the text and examining the figures, I have found at least thirty-five such factual or typographical errors. No doubt further study will reveal additional ones. It is sad to have to be so negative about a work, which if given more care and attention to detail and less haste, might have been an outstanding contribution to the literature on African butterflies.

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Text: Manuscripts should be submitted in *triplicate*, and must be typewritten, *entirely double-spaced*, employing wide margins, on one side only of white, 8½ × 11 inch paper. Titles should be explicit and descriptive of the article's content, including the family name of the subject, but must be kept as short as possible. The first mention of a plant or animal in the text should include the *full scientific name*, with *authors* of zoological names. Insect measurements should be given in *metric units*; times should be given in terms of the *24-hour clock* (e.g. 0930, not 9:30 AM). Underline only where *italics* are intended. References to footnotes should be numbered consecutively, and the footnotes typed on a separate sheet.

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